University of Alberta

Carbon storage and decay in peatlands under varying permafrost regimes

by

Merritt R. Turetsky

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Abstract

Peatlands cover 3 – 5 % of the world's land area but store ~ 30% of terrestrial soil carbon. Peat accumulates where plant net primary production (NPP) exceeds carbon losses mainly through microbial decay. Permafrost is discontinuous across the boreal forest, but near its southern limit is limited almost exclusively to peatlands. Southern permafrost in peatlands has been melting in response to climatic warming over the past ~150 years following the Little Ice Age. Given that peatlands 1) currently serve as a major reservoir of terrestrial carbon and 2) are located primarily at northern latitudes expected to receive dramatic climate warming, my objectives are to determine the influence of permafrost melt on peatland carbon storage.

^{210}Pb-dated chronologies from peatlands across Alberta, Saskatchewan, and Manitoba show that rates of peat accumulation were 40% higher in internal lawns (areas of permafrost thaw) than in bogs (no permafrost) and frost mounds (intact permafrost). Permafrost melt stimulates carbon accumulation as peat, although regional variation in the nature of this carbon response is likely. Laboratory incubations and field-based carbon fluxes suggest that heterotrophic CO_2 respiration increases following thaw. Methane emissions across the peatland surface to the atmosphere also were elevated in internal lawns compared to bogs and frost mounds, but overall fluxes were low compared to previous studies. Increased peat accumulation and heterotrophic respiration in internal lawns points to high rates of NPP post-thaw. Mass losses of

Sphagnum riparium, a common bryophyte in internal lawns, were greater than other moss species during a 1-year, field incubation. Concentrations of water-soluble carbohydrates were a strong predictor of bryophyte decay, and were higher in *S. riparium* tissue than in other mosses. *Sphagnum riparium* is allocating more of its carbon resources to the production of metabolic carbohydrates than other mosses, most likely to sustain high NPP.

Across Alberta, Saskatchewan, and Manitoba, I estimate that permafrost melt in peatlands creates an enhanced regional net sink of 160 ± 50 Gg C yr^{-1}. Future permafrost thaw may serve as a small buffer against carbon losses in peatlands due to increased fire severity and land-use (peat extraction, oil sand mining, hydroelectric reservoir creation).

Acknowledgments

I gratefully acknowledge the assistance and guidance of the 'three wise men': Dale Vitt, Kelman Wieder, and Vince St. Louis. They have provided valuable advice on field, laboratory, and statistical work, and also guided me through a stressful job market.

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Chapter 1. Introduction

Peatland carbon stocks

Peatlands represent a large global carbon (C) stock, estimated at 397-455 Pg (1 Pg $=10^{15}$ g) C (Gorham 1991; Zoltai and Martikainen 1996) or one-third of the world's soil C pool. This C has accumulated in peatlands slowly over thousands of years since the last deglaciation (Harden *et al.* 1992). Carbon accumulation in peatlands represents the balance between CO_2 fixation by net primary production and dissolved/gaseous C releases throughout the entire peat column (Figure 1). In general, peat accumulation occurs because cool wet conditions in peatlands limit decomposition (Malmer 1986; Vitt 1990). Regional rates of peat accumulation, however, are not uniform in all peatlands and are dependent upon moisture, soil temperatures, reduction-oxidation conditions (Reader and Stewart 1972; Clymo 1984), and species composition (Malmer 1986; Johnson and Damman 1991). Additional local or landscape factors, including litter quality (Yavitt and Lang 1990; Valentine *et al.* 1994; Updegraff *et al.* 1995; Yavitt and Wieder 1997), acidity/alkalinity (Szumigalski and Bayley 1997; Thormann and Bayley 1997; Thormann *et al.* 1999), nutrient availability and geomorphology (Bauer 2002) also may control peat accumulation.

Global warming is predicted to be most pronounced at northern latitudes (Raisanen 1997; Moore *et al.* 1998). Therefore, understanding how peatland C cycling is controlled by climate will be important in predicting the future response of boreal C stocks to greenhouse gas-induced warming (Gorham 1994; Svoboda 1994; Updegraff *et al.* 1995; Moore *et al.* 1998). Estimates of C stored in peatland

vegetation and organic soils are dependent upon measurements of peatland area as well as C accumulation rates or peat depth and carbon content. Peatlands cover 230-500 Mha of the earth's surface (Bramryd 1979; Kivinen and Pakarinen 1981; Franzen 1994) and today occur primarily at northern latitudes in Canada and the former Soviet Union (FSU). While Siberia and the Russian far east are thought to contain more than half of the world's boreal forest (Rugo and Weiss 1996), estimates of peatland area in the FSU vary widely from 77 to 165 Mha (Botch *et al.* 1995). Across Canada, an estimated 111 Mha, or 12% of the total land base, is covered by peatlands (National Wetlands Working Group 1988).

Uncertainty also exists in global estimates of annual C accumulation in peatlands, which range from 45 to 210 Tg C yr^{-1} (1 Tg = 10^{12} g; Bramryd 1979; Armentano 1980;). Peatland carbon stocks approach 44 Gg C in northwestern Russia (1 Gg = 10^{9} g; Kobak *et al.* 1998) and were estimated at 215 Pg C (1 Pg = 10^{15}) across the entire FSU (Botch *et al.* 1995). Carbon stored in peatlands represents 38% of the total terrestrial carbon pool in the FSU (Turner *et al.* 1998). Boreal peatlands in Canada are estimated to contain 103-184 Pg C (Ovenden 1990; Kurz *et al.* 1992; Apps *et al.* 1993), more than twice the amount stored in upland forest soils (Kurz *et al.* 1992).

The magnitude of the global peatland C sink is difficult to assess without detailed regional information on peatland aerial cover and peat depth. Estimates of global peat cover and C accumulation rates outlined above (Bramryd 1979, Armentano 1980; Kivinen and Pakarinen 1981; Franzen 1994) suggest that mean annual carbon accumulation in peatlands is between 9 and 91 g C m^{-2} yr^{-1}. Carbon

accumulation rates typically are based on radiocarbon dating and represent mean rates of accumulation averaged over hundreds to thousands of years (Turetsky and Wieder in review). Climate change most likely will affect the mass balance of C at or near peat surfaces, because deeper peat is well insulated from changing air temperatures. Therefore, it is important to focus research efforts on C cycling of recently accumulated peat.

Peatlands of western continental Canada

Extensive mapping of peatlands in western Canada has led to detailed inventories of C stocks across the western provinces of Alberta, Saskatchewan, and Manitoba (Vitt *et al.* 2000a). Here 21% of the landbase, or over 365,000 km^2, is covered by peatlands that store 42 Pg of C as peat and living biomass (Vitt *et al.* 2000a). Long term accumulation rates based on radiocarbon dating average 19.4 g C m^{-2} yr^{-1}, suggesting that regional C accumulation approaches 7.1 Tg C yr^{-1} (Vitt *et al.* 2000a).

Continental peatlands of western Canada actually are a heterogeneous mosaic of peatland types, including ombrotrophic bogs, minerotrophic fens, and permafrost features (palsas, peat plateaus and frost mounds) (Zoltai 1995; Vitt *et al.* 1994). About 63% of continental peatlands are fens, including both open, shrubby, and treed cover types (Vitt *et al.* 2000). Ombrotrophic bog islands form within larger fen complexes mainly due to changes in hydrological flow such as stagnation or water divergence (Vitt *et al.* 1994). Differences in water and nutrient availability among peatland types certainly will influence peat accumulation.

Permafrost in peatlands

Approximately 28% of peatlands in continental western Canada are underlain by permafrost and store about 13 Pg of soil C. Permafrost occurs in earth materials with temperatures below 0 °C for two or more years (Thie 1974; Woo *et al.* 1992). Permafrost distribution ranges from continuous coverage in the northern Continuous Permafrost Zone to localized permafrost landforms or frost mounds (Beilman *et al.* 2001) in the Localized Permafrost Zone (Zoltai 1995). Near the southern limit of permafrost in the boreal forest, permafrost is restricted mostly to ombrotrophic peatlands. The peat surface of these permafrost landforms is dry, as soils are elevated above the surrounding soil surface through the volume expansion of freezing soil water (Kolchugina and Vinson 1993; Zoltai 1993; Vitt *et al.* 1994; Williams and Burn 1996). Species that thrive well above the water table dominate permafrost systems, including *Picea mariana*, *Pleurozium schreberi*, *Hylocomium splendens*, *Sphagnum fuscum,* and *Cladina* spp. (Zoltai 1993; Bubier *et al.* 1995).

The insulative properties of *Sphagnum*-peat and high albedo of lichen mats in boreal permafrost peatlands allow soil ice to persist under climatic conditions that would not support permafrost in other soil types (Koster 1995; Halsey *et al.* 1995). Thus, the current distribution of discontinuous permafrost is not in equilibrium with regional climate. Other local factors, such as snow cover and the distribution of heat by water bodies, also may be important in control permafrost distribution in boreal peatlands (Halsey *et al.* 1995).

Internal lawns – new peatland features

Permafrost in western Canada reached its southernmost Holocene extent during the Little Ice Age (Vitt *et al.* 2000b), a cold climatic event in recent Earth history. However, the distribution of discontinuous permafrost in Canada's boreal forest was more extensive in the past than at present (Halsey *et al.* 1995). Localized permafrost in peatlands is degrading through its range creating wet depressions on the landscape called internal lawns (Zoltai 1993; Vitt *et al.* 1994, Vitt *et al.* 2000b). Internal lawns are wet fens initially colonized by semi-aquatic *Sphagnum* mosses and *Carex* species. During permafrost melt, *Picea mariana* roots are flooded causing tree death. Surviving trees tilt with soil subsidence, causing patterns of wood compression that can be dated through dendrochronology. Such data suggest that permafrost melt in western peatlands began around the 1890s (Vitt *et al.* 1994), concurrent with climatic warming after the Little Ice Age (Thie 1974), and continues today. Thus far, the current southern permafrost limit in western Canada has moved northwards by an average of 39 km (Beilman *et al.* 2001).

As localized permafrost in peatlands exists in disequilibrium with regional climate, the collapse of permafrost near its southern limit is occurring in areas where permafrost cannot redevelop. Strong relationships between the regional extent of permafrost collapse and mean annual temperatures suggest that permafrost degradation in the localized permafrost zone is related to an ongoing recent warming of the southern boreal forest (Vitt *et al.* 1994; Halsey *et al.* 1995). Increased fire activity across the region may also control permafrost instability (Thie 1974; Zoltai 1993). Future ice thaw in peatlands could have dramatic effects on thermokarst

development, hydrologic regimes, and C storage in boreal regions (Gorham 1991; Koster 1995; Laberge and Payette 1995; Camill and Clark 1998; Turetsky *et al.* 2000).

Canada's discontinuous permafrost zone represents a region adjusting to recent and ongoing climate change, and is ideal for examining the influence of climate on peat accumulation. Differences between peatland features, such as species composition, hydrology, thermal regimes, and nutrient status, offer a unique opportunity to investigate abiotic and biotic controls on C accumulation. The spatial heterogeneity of peatlands within the discontinuous permafrost zone adds complexity to the question of the future role of peatlands as either sinks or sources of greenhouse gases to the atmosphere, and hence either positive or negative feedbacks to global climate change.

Research Objectives

The overall goal of my research is to document variability in the relationship between peat accumulation and decomposition in heterogeneous peat deposits located in the discontinuous permafrost zone of western continental Canada. Previous studies in discontinuous permafrost have focused on direct measurements of C gas fluxes across the peatland/atmosphere interface (Bubier *et al.* 1995; Liblik *et al.* 1997; Bellisario and Moore 1998). There is little information, however, on the nature of near-surface organic matter accumulation, particularly in sites underlain by permafrost or in sites where permafrost has degraded.

Recent rates of peat accumulation

Preliminary investigations suggest that permafrost melt increases rates of peat accumulation over the past 150 years by 60% in a single peatland complex located in northern Alberta (Turetsky *et al.* 2000). In chapter two, I determine whether this pattern of increased C storage following permafrost melt is consistent on a larger scale. Rates of C accumulation in peatlands affected by permafrost melt were quantified along an east-west gradient across western Canada (Figure 1-2), using ^{210}Pb-dating (Turetsky and Wieder in review; Zoltai *et al.* 1998; Wieder *et al.* 1994). Peat cores collected in intact frost mounds, internal lawns (representing recent permafrost melt) and continental bogs were ^{210}Pb-dated, allowing me to assess the influence of intact permafrost and permafrost thaw on peat accumulation over the past 100-150 years. Because the presence, absence, or degradation of permafrost changes hydrology, nutrient inputs, and species composition, I expect the three peatland features (bogs, frost mounds, and internal lawns) to differ in patterns of near-surface organic matter accumulation.

H_1: rates of peat accumulation over the past ~100 years are greater in internal lawns than in unfrozen bogs or frost mounds due to higher rates of NPP and/or lower rates of decomposition following permafrost melt.

H_2: rates of peat accumulation are lower in frost mounds than in unfrozen bogs because dry soil surfaces in permafrost peatlands lead to high rates of decomposition.

Carbon mineralization

Peat accumulation in northern wetlands largely is driven by low rates of organic matter decay in cool, moist habitats. Chapter three deals with 1) laboratory rates of C production by peat collected from internal lawns, frost mounds, and unfrozen bogs near Patuanak, Saskatchewan, and 2) field measurements of gaseous C fluxes across the peatland-atmosphere boundary (hereafter referred to as peatland surface fluxes) in these peatlands features (Figure 1-3). Laboratory rates of C production reflect primarily the microbial production of CO_2 and CH_4 (Figure 1-1). Field-based CO_2 fluxes using dark static chambers include respiration from living aboveground and belowground plant parts (mosses, sedges, short-statured shrubs) as well as aerobic and anaerobic microbial activity within the peat column, while CH_4 field fluxes represent the balance between anaerobic production by methanogenic bacteria and oxidation by methanotrophic bacteria (Figure 1-1). Laboratory and field-based measurements of C production generally provide information about the quantities of decomposition end-products released to the atmosphere, and the potential contribution of peatlands to greenhouse gas emissions (Bellisario and Moore 1998). Permafrost degradation influences water availability and temperature relations both locally and regionally (Woo 1990; Gavrilova 1993), and therefore will affect rates of decomposition.

H_1: internal lawns will have lower rates of CO_2 production in both laboratory and field settings than unfrozen bogs and frost mounds, as internal lawn microbial metabolism will be largely anaerobic following permafrost melt. Anaerobic

metabolism is less efficient in the breakdown of organic matter than aerobic microbial metabolism (Figure 1-1).

H_2: internal lawns will have higher rates of CH_4 production in laboratory and field settings, as higher water tables and peat moisture contents following permafrost melt will favor methanogenesis.

Controls on bryophyte decay

Chapter four addresses potential controls on peatland decomposition, including peatland type, moss species, and microtopography (Figure 1-4; cf. Johnson and Damman 1991; Belyea and Warner 1994). My objective here is to investigate whether decomposition is regulated by 1) bryophyte species: five *Sphagnum* species, one feather moss, and one brown moss species, 2) peatland type: bog, poor fen, extreme rich fen, and frost mound with lateral thaw pools, 3) microtopography: dry hummocks versus wet hollows, or 4) a combination of these main effects. Peat traps filled with individual moss species were reciprocally transplanted into multiple hummock and hollows of each peatland type (Figure 1-4). I collected a subset of these samples after 1-yr of *in situ* incubation and quantified loss in dry mass over time. Decomposition rates during this field incubation were related to peat moisture contents and concentrations of recalcitrant and labile C compounds.

H_1: Bryophyte decomposition will be slower in the bog and poor fen than in the rich fen or frost mound sites, as acidity will limit heterotrophic respiration

H_2: Bryophyte decomposition will be slower in hollows than in hummocks, as high moisture availability will limit heterotrophic respiration

H_3: Bryophyte decomposition will be higher in frost mounds than in other incubation sites, as the dry soil surfaces of permafrost peatlands will favor aerobic microbial metabolism

H_4: Concentrations of labile carbon compounds in bryophyte tissue will be more important predictors for decomposition rates than recalcitrant compounds. Carbon-carbon bonds in labile carbon compounds (water-soluble carbohydrates and phenolics) are easily broken and yield greater amounts of energy than bonds in recalcitrant compounds (lignin or holocellulose). Labile compounds, therefore, yield high metabolic energy to soil microbes and will be decomposed preferentially in organic matter.

Contemporary regional C budget

Chapter five deals with the cumulative impacts of natural and anthropogenic disturbances on peatland C stocks. Permafrost melt is only one disturbance affecting peatlands across the boreal forest. Other peatland disturbances in western Canada include fire, reservoir creation, peat harvesting, linear disturbances, and oil sand mining. The cumulative impact of these disturbances on peatland C stocks has not been evaluated and must be understood to protect C sinks across boreal regions.

While peatlands generally are thought to be net sinks for atmospheric C, peatland C budgets largely are constructed for pristine systems on small spatial scales. In this chapter, I use previously published, detailed peatland inventories (Vitt *et al.* 2000a) and documented levels of current disturbance (fire, Stocks *et al.* in review; permafrost melt, cf. Vitt *et al.* 2000b) and development (reservoir creation, cf. St. Louis *et al.* 2000; Kelly *et al.* 1997; peat harvesting, Statistics Canada 1997; oil sand mining, Oil sands mining land use committee 1998) across western, continental Canada to provide the first cumulative assessment of disturbance on peatland C storage. My objectives are to 1) to extrapolate the effects of permafrost melt on peatland C accumulation across regional scales, and 2) determine whether permafrost melt is a regionally significant disturbance in western boreal Canada by comparing it to other ongoing disturbances and land-uses.

H_1: The majority of disturbance and land-use currently affecting boreal peatlands will cause net losses of C to the atmosphere through peat export/removal and changing plant and microbial production.

H_2: Permafrost degradation across western Canada partially will compensate for peatland C losses caused by disturbance and land-use by enhancing rates of peat accumulation.

Summary

Chapter six is a brief summary addressing the impacts of permafrost melt on peatland C accumulation and decomposition. Integrating information contained within chapters two through four, I provide an overview of the changes in C stocks and fluxes caused by permafrost melt. Also, by drawing upon the regional C budget described in chapter five, I outline how future climate warming may impact peatland C stocks throughout the discontinuous permafrost zone, placing these predictions into context among other disturbances within the managed boreal forest.

Figure 1-1. Schematic of the peatland carbon cycle. Through primary production, peatland vegetation fixes atmospheric CO_2 and/or soil or plant respired (i.e. refixed) CO_2 (Turetsky and Wieder, 2000). A portion of the newly fixed carbon is transferred to belowground biomass where dissolved organic carbon may be leaked by root exudation to the surrounding environment (Crow 2001) and lost to aquatic systems through runoff. Aerobic and anaerobic decomposition transforms solid and dissolved organic carbon into gaseous byproducts (CO_2 and CH_4) that diffuse to the atmosphere. Methane produced at depth in the catotelm (permanently saturated zone) by methanogens may be oxidized by methanotrophic bacteria in the acrotelm (permanently unsaturated region zone and zone of fluctuating water table). Decomposition in the acrotelm occurs at rates faster than in the catotelm due to greater efficiency of aerobic versus anaerobic metabolism. Fire releases greenhouse gases to the atmosphere through organic matter combustion.

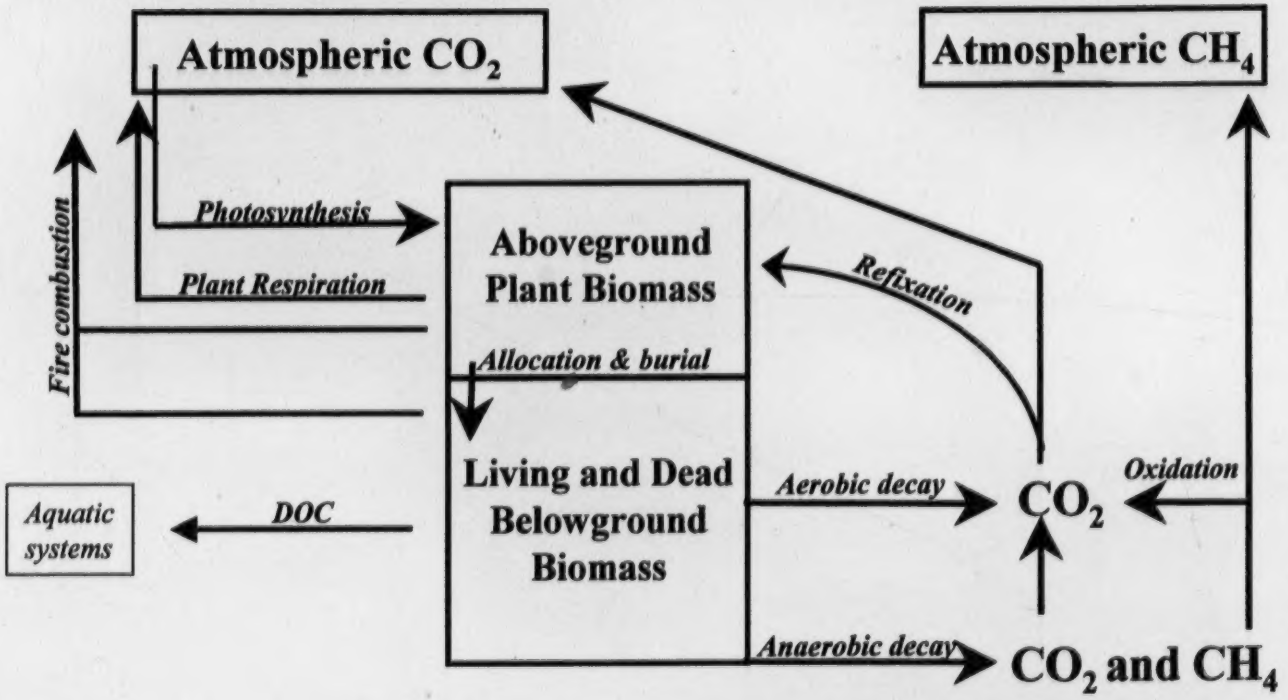

Figure 1-2. Map of north America (left) with western continental Canada outlined in heavy black. Peatland sites (right) along an east-west transect near the southern limit of permafrost across western continental Canada (Vitt *et al.* 2000). At each site, peat cores were collected in each of three bogs (no permafrost), frost mounds (intact permafrost), and internal lawns (melted permafrost),and were brought back to the University of Alberta where they were processed for soil dating procedures (Chapter 2).

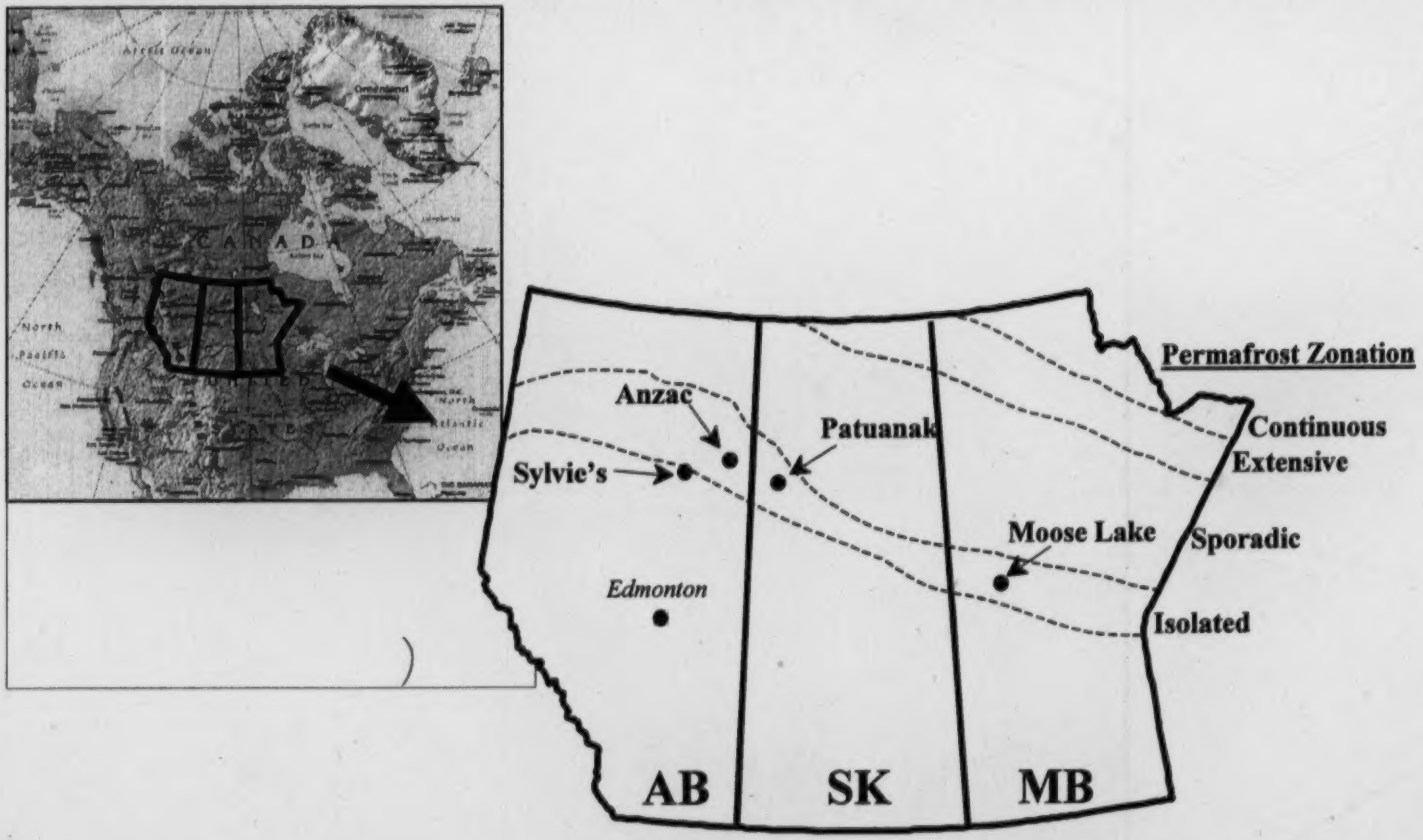

Figure 1-3. Map of western, continental Canada (Alberta, Saskatchewan, Manitoba) showing the location of the study area in central Saskatchewan, and a schematic outlining my sampling design (after Vitt *et al.* 2000). I quantified ecosystem C respiration for three sites, each of which contained an isolated frost mound (FM), an internal lawn (IL) and a continental bog (CB). Also, I quantified potential rates of C mineralization in the laboratory from surface and deep peat collected within features of each site.

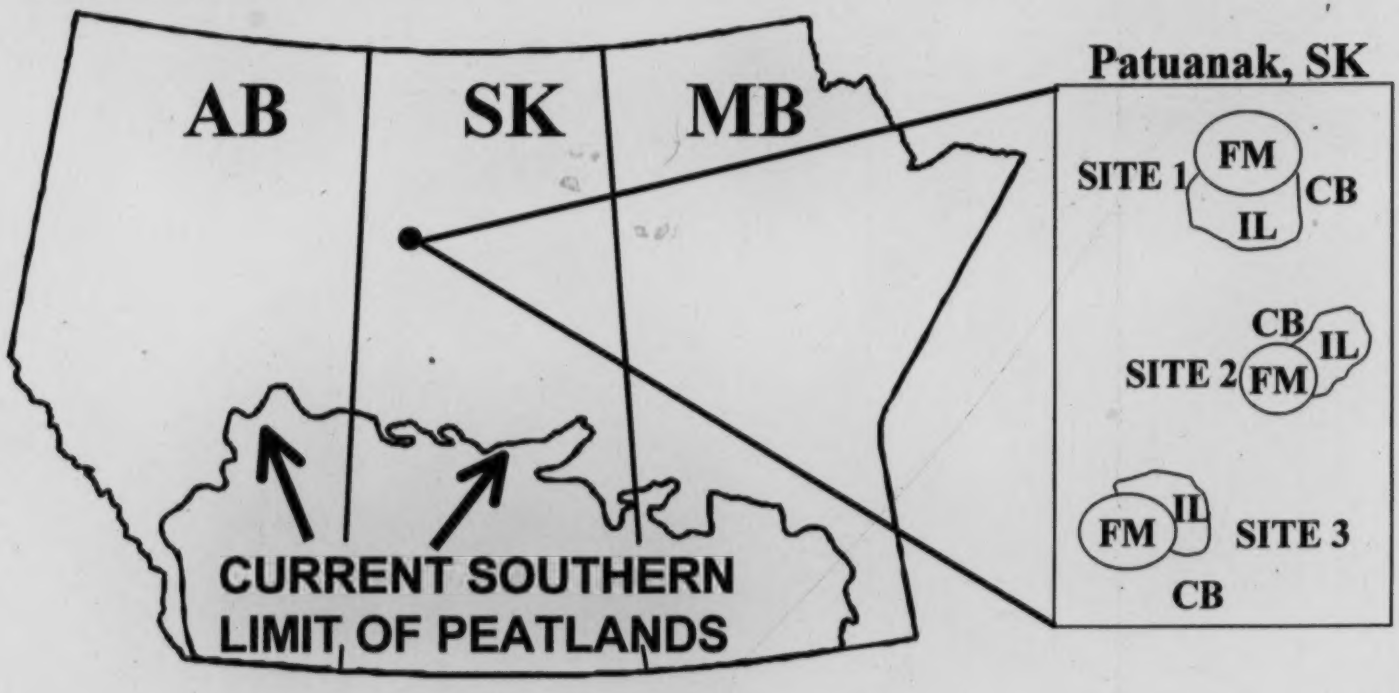

Figure 1-4. Schematic of a decomposition study evaluating the influence of moss species, microtopography, and peatland type on *in situ* rates of mass loss. We harvested eight bryophyte species (original location of collection in parentheses), including a common hummock (hum) and hollow (hol) species from a bog (B), poor fen (PF), rich fen (RF), and frost mound with thaw (FM). Eight bryophyte species were reciprocally transplanted into both hummocks and hollows of four peatland types that differed widely in moisture availability and acidity.

I. Species	II. Topography	III. Peatland Types
Sphagnum mosses		
S. magellanicum (PF hum)		
S. jensenii (PF hol)	Hummocks	Extreme rich fen: ***Calcareous, Wet***
S. fuscum (B hum)		
S. angustifolium (B hol)		Poor fen: ***Acidic, Wet***
S. riparium (FM hol)		
		Bog: ***Acidic, Dry***
Brown/feather mosses		
Tomenthypnum nitens (RF hol)	Hollows	Frost mound: ***Dry***
Scorpidium scorpiodes (RF hum)		
Pleurozium schreberi (FM hum)		

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Chapter 2. Permafrost thaw and soil carbon storage in western boreal peatlands

Introduction

Carbon stocks in boreal regions

Terrestrial boreal ecosystems globally cover 7-14 million km^2 of forested land, representing about 20 % of the Earth's land area (Apps *et al.* 1993; Scott 1995; Zoltai and Martikainen 1996; Goldhammer and Stocks 2000). Located at high latitudes (~ 47 - 70 ° N latitude), boreal regions are characterized by cold winters, relatively low solar insolation, and short growing seasons (< 90 frost-free days). While precipitation varies widely between coastal and continental areas, annual precipitation across much of North America's boreal forest is low (< 300 mm). Thus, the southern boundary of western boreal regions tends to be controlled by soil moisture (Hogg 1994).

Forested boreal ecosystems contain about 40 % of the world's terrestrial carbon (C; Apps *et al.* 1993), stored mostly in deep soil deposits of organic debris or peat (Vitt *et al.* 2000). Low rates of decomposition caused by saturated, cool soils and poor litter quality lead to the buildup of litter and soil organic matter. The slow accumulation of C in boreal soils represents a long-term sink of atmospheric C since glacial retreat in North America between 8-12 thousand yrs ago (Harden *et al.* 1992). Today boreal systems represent one of the largest terrestrial C reservoirs, and thus exert a strong influence on C exchange between terrestrial biota and the atmosphere (Dixon *et al.* 1994).

Permafrost and peat

The majority of land in northern regions is affected by permafrost, *i.e.* earth materials remaining at or below 0 °C for two or more yrs (Thie 1974). Permafrost

distribution at northern latitudes ranges from continuous coverage in arctic and subarctic regions, to discontinuous or sporadic distributions further south in the boreal. At its southern limit, sporadic permafrost is limited almost exclusively to boreal peatlands where deep deposits of organic matter and black spruce canopies promote and insulate frost layers. These isolated frost mounds are in disequilibrium with current climate, representing relict features of the Little Ice Age (recent cold climatic event that ended approximately 250 yr ago) that have been preserved by insulating peat (Vitt *et al.* 1994; Halsey *et al.* 1995). Since the maximum spatial extent of permafrost during the Little Ice Age, permafrost in peatlands near its southern limit has been degrading across much of North America (Vitt *et al.* 2000; Beilman *et al.* 2001). Permafrost thaw creates wet depressions called internal lawns that are surrounded mainly by unfrozen peatlands and are dominated by wet adapted *Sphagnum* and *Carex* species. Internal lawns are found across the boreal forest of North America, suggesting regional patterns of permafrost thaw caused by fluctuating climatic conditions.

Dating peat deposits

Peat deposits are highly organic, often 95 % organic matter or greater on a dry mass basis, especially in ombrotrophic bogs, which receive water and inorganic nutrient inputs solely from atmospheric deposition. *Sphagnum*-derived peat in bogs and poor fens has a high cation exchange capacity, which has been attributed to high concentrations of unesterified polyuronic acids in *Sphagnum* cell walls (Spearing 1972). Through cation exchange, positively charged ions sorb strongly to the negatively charged functional groups on peat (Rapaport and Eisenreich 1986; Livett

1988; Clymo *et al.* 1990; Cole *et al.* 1990; Wieder 1990; Vile *et al.* 1999). This may immobilize cations that are deposited via dry or wet deposition or via surface/ground water flow (fens only) in the peat column. Unlike lake sediments, in which the record of deposition may be distorted by varying rates of particle sedimentation, multiple source inputs, and bioturbation, peatlands often are ideal archives of atmospherically deposited cations/particulates due to cation exchange and the ombrotrophic nature of bogs (Clymo *et al.* 1990).

Because of ongoing decomposition and compaction within a peat deposit, depth generally is not linearly related to age (Clymo 1984; Clymo *et al.* 1990). Accurate dating of a peat profile is essential to construct chronologies from which rates of historical contaminant loading or organic matter accumulation can be calculated. Many commonly used dating methods take advantage of the ombrotrophic nature of some peatlands (Turetsky and Wieder in review). These dating approaches rely on the assumption of post-depositional immobility of atmospherically derived constituents mainly through cation exchange (Shotyk *et al.* 1997a; Vile *et al.* 1999). Large, nonpolar compounds (such as PCBs and PAHs) also bind strongly to the organic peat matrix (Rapaport and Eisenreich 1988; Sanders *et al.* 1995). Such strong binding limits mobility of certain atmospherically-deposited materials within peat.

Based on the radioactive decay series of ^{238}U, ^{210}Pb-dating (Goldberg 1963; Appleby and Oldfield 1978) allows for radiometric dating of peat formed over the past 150-200 yrs. Uranium-238 is a primordial nuclide, present since the earth first condensed into a solid mass some four billion yrs ago. Because of its long half-life (4.46×10^9 yr), about half of the original ^{238}U remains today. Widely dispersed in the earth's crust, ^{238}U is found in all sediments and continually is decaying to produce

^{210}Pb and other daughter isotopes. The total ^{210}Pb pool in soil, sediment, or peat has two components: 1) a supported ^{210}Pb component produced within the soil via radioactive decay of ^{222}Rn that never diffused to the atmosphere, and 2) an unsupported ^{210}Pb component derived from ^{222}Rn that first diffused into the atmosphere and subsequently decayed to ^{210}Pb. Unsupported ^{210}Pb, removed from the atmosphere via wet deposition and dry fallout, is deposited onto the earth's surface. Mean global ^{210}Pb flux onto land surface has been estimated at 166 Bq (a becquerel is equivalent to one disintegration per minute) m^{-2} yr^{-1} (Krishnaswami and Lal 1978), but varies among sites. Estimates of unsupported ^{210}Pb deposition to the earth's surface, calculated from the integrated ^{210}Pb inventory in peat deposits, have ranged from 95 to 329 Bq m^{-2} yr^{-1} (Schell 1986; Schell *et al.* 1986; Urban *et al.* 1990; Belyea and Warner 1994; Norton *et al.* 1997; Appleby *et al.* 1997; Vile *et al.* 2000).

Pb-210 dating may allow for construction of a continuous dating record extending back to generally no more than about 150 yr from the present (time of core collection). After 10 half-lives ($T_{1/2}$ = 22.3 yr) or about 223 yr, unsupported ^{210}Pb concentrations cannot be detected against a background of supported ^{210}Pb.

Pb-210 dating assumes immobility of atmospherically deposited ^{210}Pb at the peat/sediment surface and subsequently within the peat profile over time (von Gunten 1995; Shotyk *et al.* 1997b; Vile *et al.* 1999). Several studies have invoked mobility of Pb in peat to explain vertical distributions of Pb in peat columns (Damman 1978; Clymo and Hayward 1982; Pakarinen *et al.* 1983; Urban *et al.* 1990; Oldfield *et al.* 1995; Sanders *et al.* 1995). However, others have more definitively concluded that Pb remains immobile after deposition onto a peat surface (Benninger *et al.* 1975; Livett *et al.* 1979; Mitchell *et al.* 1992; Appleby *et al.* 1997; Farmer *et al.* 1997; MacKenzie *et*

al. 1997; Vile *et al.* 1999) or have found good agreement between ^{210}Pb-dating in peat cores and other dating methods or date markers (El-Daoushy *et al.* 1982; Clymo *et al.* 1990; Cole *et al.* 1990; Belyea and Warner 1994; Wieder *et al.* 1994; Vile *et al.* 1995; Appleby *et al.* 1997; MacKenzie *et al.* 1997; Shotyk *et al.* 1997b)

Boreal ecosystems and global warming

Northern ecosystems are expected to receive the most drastic warming under an enhanced-CO_2 atmosphere, with expected temperature increases of up to 5 °C (Raisanen 1997; Moore *et al.* 1998). Wetlands systems, such as peatlands and prairie potholes, also are vulnerable to climatic fluctuations as they depend on water saturated conditions (Burkett and Kusler 2000; Kettles and Tarnocai 1999). Already over the past several decades, portions of the circumboreal ecoregion have warmed between 0.2 – 2 °C (Kasischke and Stocks 2000), at least partly in response to greenhouse gas loading in the atmosphere (Mitchell and Karoly 2001; Stott *et al.* 2000). While precipitation patterns will not change homogenously across North America, much of the boreal forest is expected to receive less precipitation in the future (Stocks 1998).

Global change is predicted to have strong influences on patterns of C storage and soil structure in northern wetlands. Drier and warmer soil conditions will lead to an enhanced oxidation of stored organic matter to CO_2, and will increase rates of CH_4 oxidation (Moore *et al.* 1998; Figure 1-1). Climate warming also will have indirect impacts on C stocks if it 1) leads to warmer permafrost and accelerated thaw, and/or 2) increases fire severity and occurrence in boreal regions (Kurz and Apps 1999; Murphy *et al.* 2000).

Predicting both the direct and indirect impacts of future global change on northern peatland C storage may not be straightforward. Increasing winter and/or growing season temperatures may accelerate biological processes such as plant and microbial metabolisms and will lead to thicker active layers (depth of seasonal melt). Shallow snowpacks, however, may lead to colder soils in winter months, allowing frost to penetrate deeper into soil layers. Changing patterns of winter precipitation also will influence the extent of spring runoff, while summer precipitation will influence soil moisture and runoff throughout the growing season (Schindler 2001). Disturbances such as fire, which also is expected to increase in northern continental regions over the next several decades (Stocks 1998), almost certainly will have severe consequences for existing permafrost landforms (Swanson 1996; Chapter 5).

Several authors have predicted that permafrost degradation would lead to positive feedbacks on greenhouse warming through the mineralization of previously frozen organic matter to CO_2 and CH_4 (Gorham 1991; Kettles and Tarnocai 1999). However, more recent studies have reported that permafrost thaw stimulates rates of organic matter accumulation (Robinson and Moore 2000; Camill 1999; Turetsky *et al.* 2000), with the potential to enhance ecosystem C storage at northern latitudes. The majority of work thus far has focused on "collapse scar" features located farther north than the southern limit of permafrost. The presence of northern collapse scars in larger permafrost features such as peat plateaus may be indicative of cyclical aggradation/degradation in response to fire (Zoltai 1995) or alternatively, permafrost may never have accumulated in these scar areas. Here I focus on patterns of thaw near the southern limit of permafrost. The collapse of sensitive, isolated permafrost landforms (frost mounds), creating wet, *Sphagnum*-dominant internal lawns, has

occurred and continues to occur across most of North America in response to climatic warming over the past few centuries. At some depth in an internal lawn, transition to sylvic peat that characterized the former permafrost feature always is present. Here, my research objective is to use ^{210}Pb-dating to document patterns of peat accumulation over the past 50-100 yr in peatlands across the southern limit of permafrost in western Canada, including unfrozen treed bogs, frost mounds with intact permafrost, and internal lawns, representing recent permafrost thaw.

Methods

In collaboration with Kelman Wieder (Villanova University) and Joseph Yavitt (Cornell University), I established a broad regional transect across the discontinuous permafrost zone of western Canada including four peatland complexes (Figure 1-2; Table 2-1). These peatland complexes were identified using aerial photography with two criteria: 1) internal lawn presence, identified from the photographs as wet depressions on the landscape with no or few living trees, and 2) close access to road structures. All sites were within walking distance, i.e. several kilometers, from the nearest road. Within each internal lawn site, the collapse of permafrost was verified by identifying a transition from sylvic, dense peat to Sphagnum riparium material with the peat column.

Data from the Sylvie's bog site are published in Turetsky *et al.* (2000), but are included in this study for regional comparison. At the Anzac, Mooselake, and Patuanak sites, two replicate peat cores were collected from multiple bogs, frost mounds, and internal lawns using 1-m long PVC cylinders (10 cm diameter) with sharpened bottom edges. Cores were collected with care to ensure minimal

compaction (less than 10 cm in bog and frost mound cores, less than 20-40 cm compaction in internal lawn cores). Cores were frozen and sectioned into 3 cm depth increments using a band saw. Individual depth increments were dried and weighed for bulk density measurements prior to homogenization with a Tecator Cyclotec sample mill. Ash concentrations were determined on subsamples of each depth increment by loss on ignition at 450 °C for 4 h.

Rates of organic matter accumulation as peat were determined via ^{210}Pb dating of cores by acid digestion and application of the constant rate of supply model (Appleby and Oldfield 1978). A 2-3 g subsample from each peat core section, along with 15 dpm (250 mBq) of ^{209}Po as a chemical yield tracer, was digested with concentrated HCl, concentrated HNO_3, and H_2O_2. The Pb and Po isotopes were passively plated onto silver disks for activity measurement on an EG&G ORTEC 576A alpha spectrometer located at Villanova University (Wieder *et al.* 1994). ^{210}Pb concentrations in peat are expected to decrease exponentially with depth, approaching a low constant value taken to represent the supported ^{210}Pb fraction, (i.e., that formed within soil) as opposed to that deposited from the atmosphere (the unsupported ^{210}Pb fraction).

I constructed rates of cumulative organic matter accumulation (ash-free) by quantifying dry mass, ash concentrations and bulk density of each depth interval within peat chronologies. For each core, accumulation rates were calculated during the past 50 and 100 yr periods, and were analysed by two-way analyses of variance (SAS 1998). Region (Anzac, Sylvie's, Patuanak, Mooselake) and feature (bog, internal lawn, frost mound) were considered main effects and Tukey's tests were used for *post hoc* comparisons of means (SAS 1998).

Results

The internal lawn and bog chronologies showed similar patterns of net vertical peat accumulation (cm yr^{-1}) (Figure 2-1). Over the past 100 yrs, bogs within my sites have accumulated 20 – 35 cm of peat, while internal lawns have accumulated 20 - 45 cm (Figure 2-1). Frost mounds had lower values, with accumulations of only 10 – 30 cm of peat over the past 100 yrs (Figure 2-1). Vertical accumulation rates in frost mounds are more variable than in the other peatland types, with abrupt discontinuities in accumulation rates.

Rates of organic matter (OM) accumulation (kg OM yr^{-1}) through time also differ between peatland features (Figure 2-2). Cumulative accumulation curves for individual peat cores over the past 100 yrs range from 11 - 22 kg OM m^{-2} in bogs, 14 - 24 kg OM m^{-2} in internal lawns, and 6 - 30 kg OM m^{-2} in frost mounds (Figure 2-2). Replicate cores collected within a single peatland feature often show variation in the rate of surface peat accumulation. However, there is more variation in organic matter accumulation among frost mound chronologies compared to the other peatland types. Individual cores collected in the Mooselake or Anzac frost mounds reach cumulative organic matter accumulations of 40-50 kg OM m^{-2} over the past 200 years (Figure 2-2).

Accumulation rates of organic matter during both a 50- and 100 yr- period exhibited a region × feature interaction (Table 2-2, Figure 2-3). At the Sylvie's and Patuanak sites, 50 yr- peat accumulation rates are higher in internal lawns than in frost mounds or unfrozen bogs. However, internal lawn accumulation is similar to that in unfrozen bogs at the Mooselake site in Manitoba, and internal lawn accumulation is

intermediate between frost mounds and unfrozen bogs at the Anzac site. Within each site, frost mounds consistently show the lowest rates of 50 yr- cumulative peat accumulation compared to the other peatland types, except at the Sylvie's peatland complex where frost mound and unfrozen bog accumulation is similar (Figure 2-3).

Generally, differences in organic matter accumulation between peatland features are less pronounced during the past 100 yr compared to trends during the past 50 yr of accumulation (Figure 2-3). At the Anzac, Patuanak, and Sylvies sites, there are no significant differences between bog, internal lawn, and permafrost accumulation. Within each site, however, mean accumulation rates among features often are associated with high standard errors (Figure 2-3).

In general, peatlands near Patuanak, SK and Anzac, AB had the highest organic matter accumulation (19.4 ± 1.2 and 18.9 ± 2.1 kg OM m^{-2} 100 yr^{-1}; respectively n=15 and 8). Accumulation was lowest at Sylvie's complex in AB (12.8 ± 1.5 kg OM m^{-2} 100 yr^{-1}; n=5). Among my western Canadian sites, organic matter accumulation over the past 100 years was highest in internal lawns (21.2 ± 0.9 kg OM m^{-2} 100 yr^{-1}; n=13) and lowest in frost mounds (15.1 ± 1.7 kg OM m^{-2} 100 yr^{-1}; n=16). Bog accumulation was intermediate and averaged (17.0 ± 0.9 kg OM m^{-2} 100 yr^{-1}; n=16). Accumulation rates following permafrost thaw were 76% and 40% higher over a 50- and 100- yr period, respectively, compared to frost mounds.

Discussion

Annual rates of peat accumulation can be estimated by directly quantifying net primary production and decomposition rates in peatlands. However, methodological limitations, combined with typically large spatial and temporal variability in plant

production and decomposition, may lead to substantial errors in extrapolating from direct measurements to annual C budgets. An alternative approach to estimating the C sink capacity of a peatland takes advantage of the longer-term records stored in peat deposits (Belyea and Warner 1994; Wieder *et al.* 1994; Oldfield *et al.* 1995; Clymo *et al.* 1998; Turetsky *et al.* 2000; Wieder 2001).

Surface peat accumulation varied among peatland complexes across western Canada (Table 2-2; Figure 2-2/3), but showed no obvious relationship between surface peat accumulation and regional climatic variables (Table 2-1). Changes in community structure occurring with environmental heterogeneity across boreal landscapes will influence ecosystem properties such as net primary production (Szumigalski and Bayley 1997, Thormann and Bayley 1997) and microbial decay (Johnson and Damman 1991, Belyea 1996, Hobbie 1996). Hydrology, substrate topography, and species composition will influence peat accumulation, and should be quantified for a mechanistic understanding of the factors controlling C accumulation as peat. A more detailed understanding of relationships between ecosystem function, species structure, and environmental and edaphic gradients will allow for better predictive assessments of the future of northern C stocks.

Here, my primary objective was to quantify rates of organic matter accumulation rates in peatlands with permafrost (frost mounds; sensu Beilman *et al.* 2001), without permafrost (bogs) and with degraded permafrost (internal lawns). While previous work hypothesized that permafrost aggradation in peatlands leads to diminished or terminated soil organic matter accumulation (cf, Zoltai 1993), these results show that frost mounds at the southern limit of permafrost are accumulating C as peat. Despite dry soil conditions above the permafrost table and an absence of acid-

generating *Sphagnum* species, frost mounds in my sites accumulate peat at rates similar to unfrozen bogs. Over the past 100 yr, frost mounds and bogs across western Canada have accumulated 17.0 ± 0.9 and 15.1 ± 1.7 kg OM m^{-2} 100 yr^{-1}, respectively.

Rates of organic matter accumulation in frost mounds showed sharp discontinuities with depth both in vertical (cm yr^{-1}) and cumulative organic matter accumulations (kg m^{-2}). These surface patterns may point to the patchy nature of vascular litter inputs over time in a permafrost environment. Although feather mosses and lichens comprise a nearly continuous ground layer, the underlying soil organic matter in frost mounds is sylvic with high amounts of input from black spruce litter. Like upland organic soil horizons, permafrost peat has thick root layers or duff mats which could contribute to heterogeneity in soil organic matter concentrations. Additionally, fire is more important to frost mounds than to surrounding peatland types due to drier soil conditions and greater fuel loads. Severe organic matter combustion in frost mounds during fire (Turetsky and Wieder 2001) also could explain the observed discontinuities in peat accumulation.

Internal lawns across western Canada have accumulated 25% and 40% more peat over the past 100 yrs compared to unfrozen bogs and frost mounds, respectively. Rates of C accumulation in collapse scars, located further north in the discontinuous permafrost zone, also show increased C accumulation compared to frozen permafrost plateaus (Robinson and Moore 2000, Camill *et al.* 2001).

Permafrost melt may serve as a negative feedback on future climate warming by stimulating soil carbon storage (Figure 2-4). However, regional variation both in the nature and magnitude of that C response seems likely. Internal lawns currently are serving as a greater net sink for atmospheric CO_2 than are frost mounds at all of my

western Canadian sites (Figure 2-3A). As internal lawns accumulate organic matter over time, increasing distance from the peat surface to the water table may drive succession from hydrophilic *Sphagnum* species to mesic and zeric *Sphagnum* species characteristic of continental bogs. Presumably, as species composition becomes more similar to bog vegetation, internal lawns will accumulate organic matter at rates comparable to unfrozen continental bogs. Therefore, a more complete understanding of 1) the timing of permafrost collapse across western Canada that creates internal lawns on the landscape, and 2) the duration of enhanced peat accumulation in internal lawns compared to bogs are needed to determine the implications of permafrost collapse on soil carbon stocks and will be an important factor in determining regional C budgets for boreal regions.

Table 2-1. Climate and peatland physiognomy of the main study regions in western Canada. Data modified from Beilman 2001. Climate data are 1951-1980 climate normals (Environment Canada. 1998) from the nearest climate station, except for mean annual temperature at Patuanak that follows interpolated means corrected for elevation due to a lack of available nearby temperature data (Vitt *et al.* 1994; Beilman 2001).

	Anzac AB	**Sylvies AB**	**Patuanak SK**	**Mooselake MB**
Mean annual temperature (°C)	-0.4	0.2	-1.0	-1.2
Mean annual precipitation (mm)	472	465	444	496
Mean permafrost landform size (ha)	0.198	NA	0.248	0.295
Extent of degradation (%)	60.3	NA	65.5	53.2

Table 2-2. Analysis of variance results conducted on 50- and 100- yr accumulation rates for peat cores collected in three peatland features (bogs, frost mounds, internal lawns) from four peatland complexes (Anzac, Sylvie's, Patuanak, and Mooselake).

Model Effects	**df**	**Type III Sum of Squares**	***F***	***p***
50 Yr Peat Accumulation				
Model	11	347052729	10.54	0.0001
Region	3	40212607	4.48	0.0094
Feature	2	146797881	24.51	0.0001
Region × Feature	6	58399686	3.25	0.0124
Error	34	448866920		
100 Yr Peat Accumulation				
Model	11	698907974	3.79	0.0014
Region	3	150661080	3.00	0.0446
Feature	2	136971038	4.00	0.0259
Region × Feature	6	249632950	2.48	0.0429
Error	33	552698119		

Figure 2-1. Peat depth/age relationships established via ^{210}Pb-dating of **A.** frost mound, **B.** internal lawn, and **C.** bog peat cores collected across western Canada. Each data point represents a single depth interval from a peat core. Increasing error bars with depth represents counting errors from alpha-spectrometry.

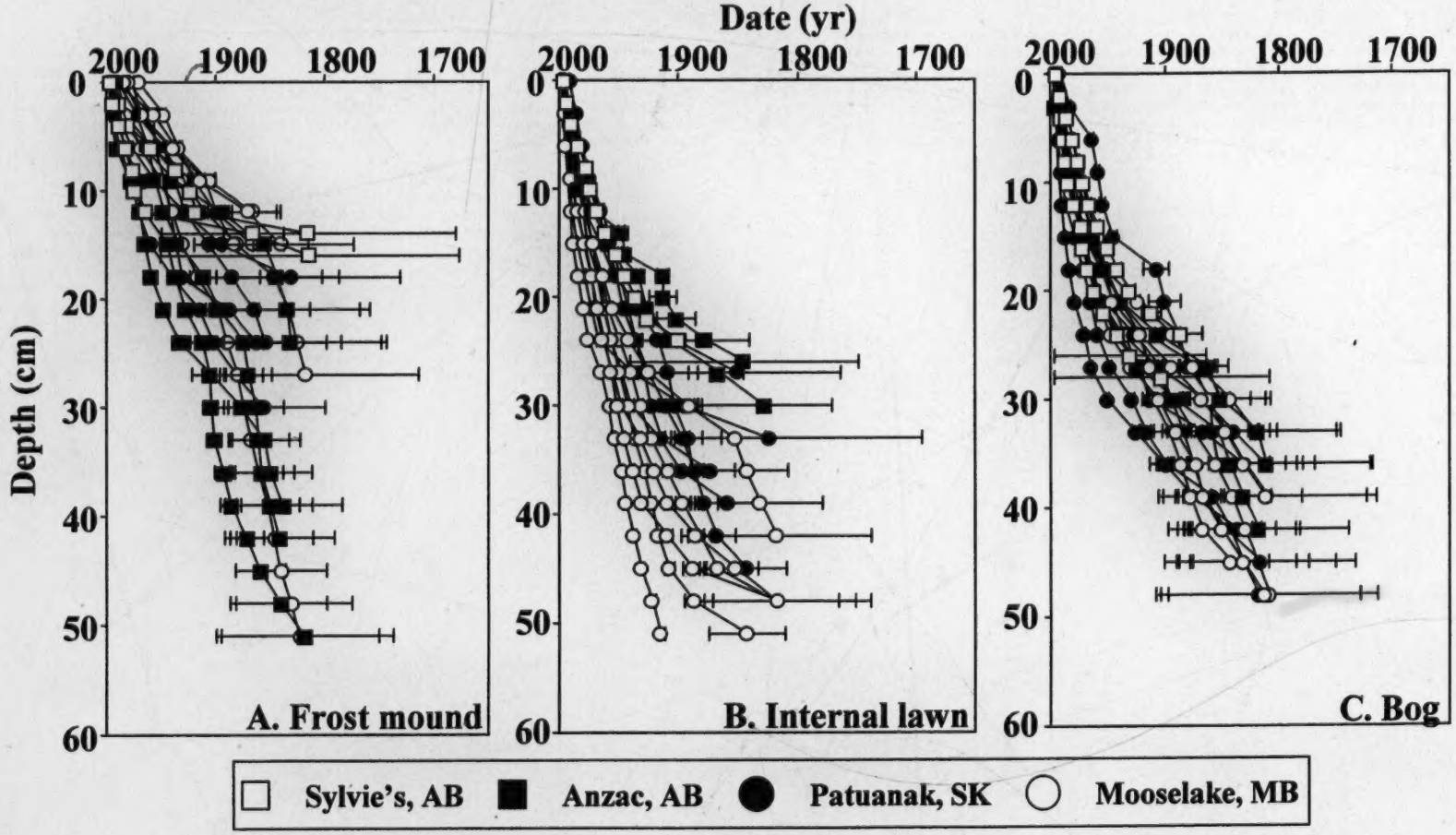


Figure 2-2. Cumulative organic matter (OM) accumulation in kg m^{-2} over time for each dated peat core, analyzed by ^{210}Pb-dating, collected from either **A.** frost mounds, **B.** internal lawns, or **C.** bogs.

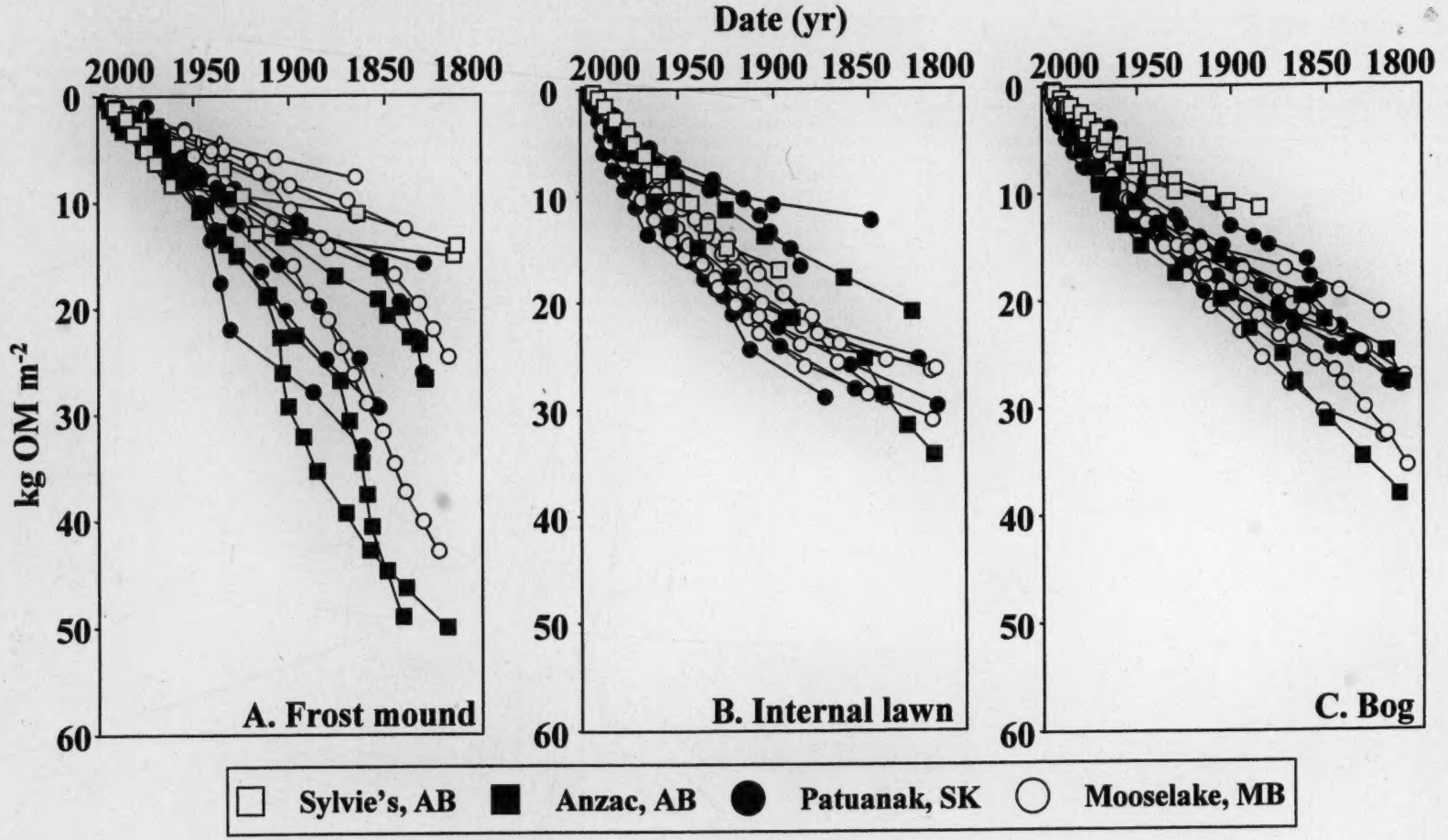


Figure 2-3. Mean organic matter accumulation for ^{210}Pb-dated bog (CB), frost mound (FM) and internal lawn (IL) cores over **A**. 50 yr and **B**. 100 yr time periods.. Means with the same letter superscript do not differ significantly (LSD; Table 2-2). 48 chronologies in total were established by ^{210}Pb-dating (n=6 for the Patuanak site, 6 for Mooselake, 2 for Anzac, and 2 for the Sylvie CB and FM and 1 for Sylvie IL).

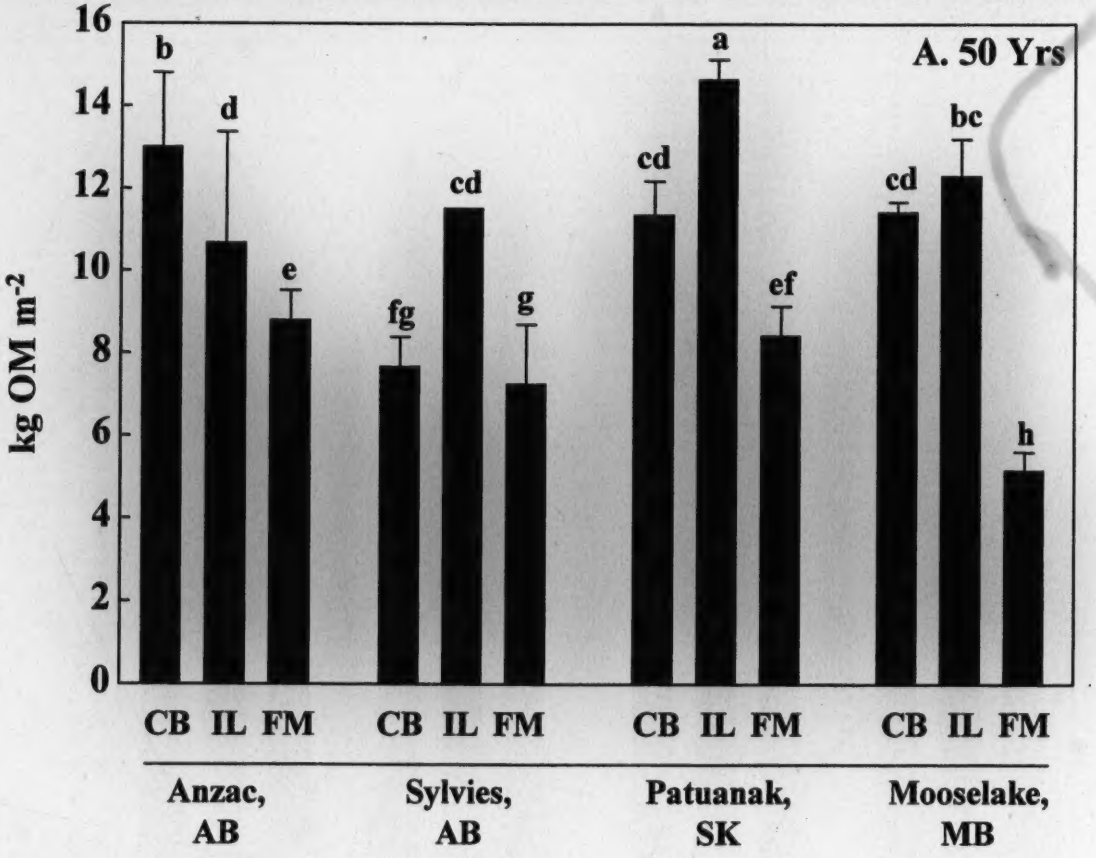


Figure 2-3 continued

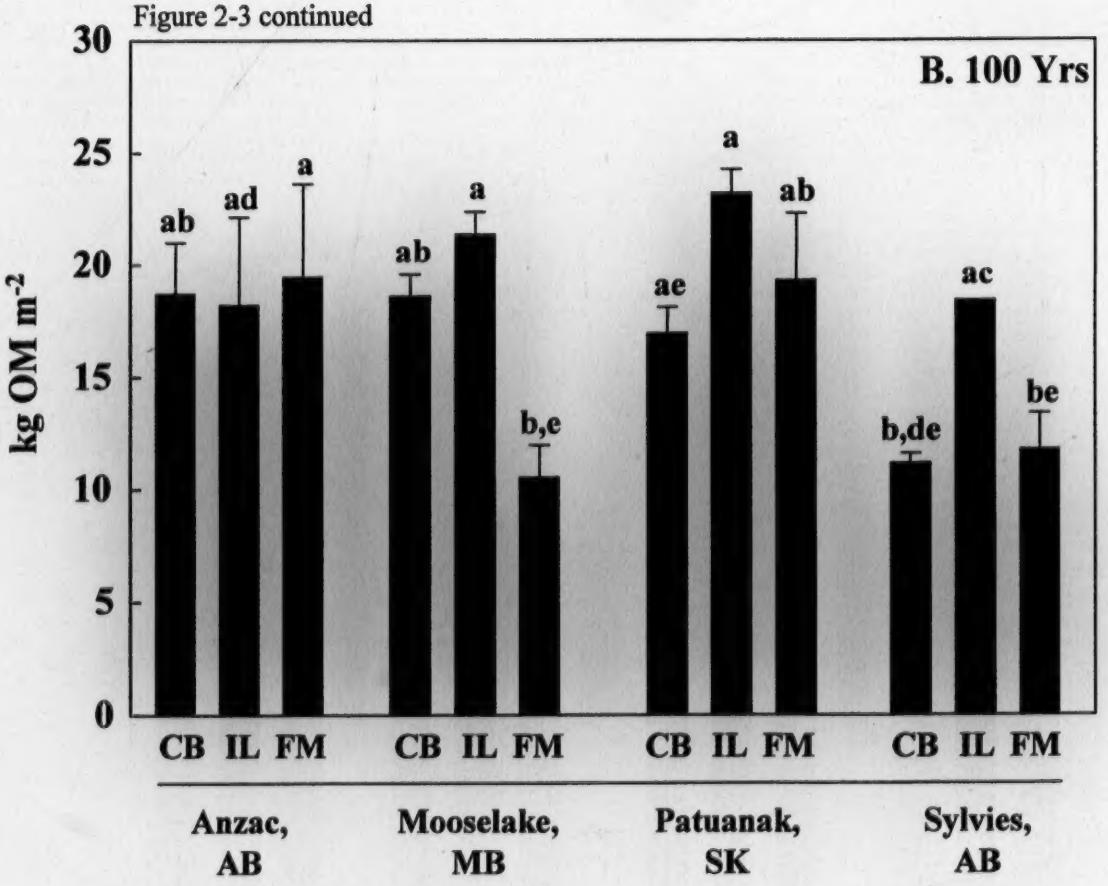
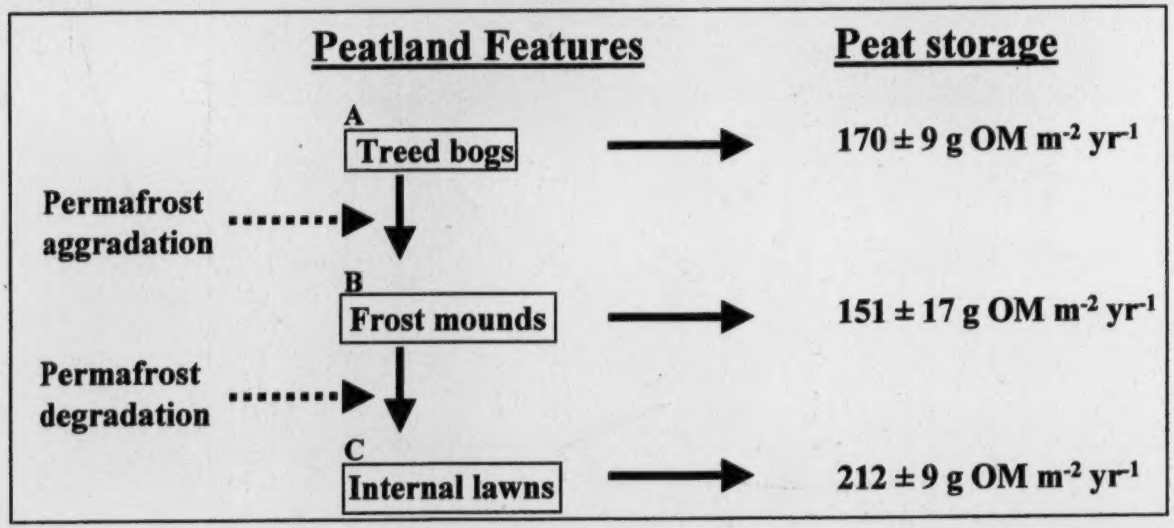


Figure 2-4. Schematic of peatland development and its influence on carbon storage in the discontinuous permafrost zone of boreal western Canada. **A)** After retreat of the Laurentide ice sheet, peatlands developed as fens on areas of poor drainage through paludification or over small water bodies through terrestrialization. Peat accumulation was initiated by slow decomposition in saturated soils, but peat accumulation above the water table led to drier local soil conditions. Invasion of *Sphagnum* species causes declining soil pH values. **B)** Following the Hypsithermal warm period (beginning about 10,000 yr BP) in western Canada, insulation caused by surface peat and/or black spruce canopies may have initiated permafrost aggradation in peatlands. Permafrost peat is comprised mainly of vascular debris accumulated under relatively dry soil conditions, yet rates of surface peat accumulation in frost mounds is similar to unfrozen bogs. **C)** Melting of discontinuous permafrost may be triggered by a recent, ongoing warming of Canada's southern boreal region. Permafrost thaw creates wet depressions called internal lawns that are dominated by wet adapted *Sphagnum* and *Carex* spp. Either through enhanced plant primary production or lower rates of decomposition, internal lawns accumulate surface peat at average rates faster than frost mounds or unfrozen bogs.



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Chapter 3. Carbon mineralization in boreal peatlands under varying permafrost regimes

Introduction

Peatlands cover over 365 000 km^2 in Alberta, Saskatchewan, and Manitoba and store about 48 Pg of C as peat and living biomass (Vitt *et al.* 2000). Within this region, about 28% of peatlands are underlain by permafrost that, in total, store 13 Pg of C (Vitt *et al.* 2000). However, permafrost distribution ranges from continuous coverage in the northern Continuous Permafrost Zone to discontinuous ice lenses in the Localized Permafrost Zone (LPZ; Zoltai 1995; Beilman *et al.* 2001). Near its southern limit in the LPZ, permafrost is restricted to ombrotrophic peatlands where insulative organic matter deposits promote ice aggradation and persistence (Zoltai 1995; Halsey *et al.* 1995; Vitt *et al.* 2000).

The maximum extent of permafrost in western Canada occurred during the Little Ice Age (Halsey *et al.* 1995). Over the past 150-200 y, temperatures across the boreal forest have increased by about 1°C (Campbell and McAndrews 1993), resulting in widespread permafrost degradation (Halsey *et al.* 1995; Vitt *et al.* 2000). Peatland surface topography collapses with ice melt, increasing water availability. Tree death, resulting from inundation of *P. mariana* roots, increases insolation (Vitt *et al.* 1994; Vitt *et al.* 2000). Internal lawns are open, relatively wet *Sphagnum-Carex* lawns that represent localized permafrost degradation (Vitt *et al.* 1994).

Peatlands globally are believed to function as a net sink for atmospheric CO_2 and as a net source of CH_4 (Roulet *et al.* 1992; Bartlett and Harriss 1993; Cao *et al.* 1998; Whalen and Reeburgh 2000). Detailed C balance studies, however, often reveal

that individual peatlands may switch annually from net C sinks to sources (Alm *et al.* 1997; Rivers *et al.* 1998; Waddington and Roulet 2000). The presence or absence of permafrost may have important consequences for C cycling in peatlands, and for our understanding of the future responses of boreal systems to climatic change. However, there are few data comparing C emissions between peatlands with differing permafrost patterns (Bubier *et al.* 1995; Liblik *et al.* 1997).

My research goal was to investigate CO_2 and CH_4 dynamics in peatlands with differing permafrost regimes on a local spatial scale in the LPZ. Here, I quantify 1) laboratory rates of gaseous C production by peat, and 2) field fluxes of CO_2 and CH_4 across the peat surface/atmosphere boundary in frost mounds (intact permafrost), unfrozen bogs (no evidence of permafrost; Vitt *et al.* 1994), and internal lawns (representing recent melt). Laboratory rates of C mineralization reflect the microbial production of CO_2 and CH_4, although root respiration may contribute to CO_2 production in surface peat, particularly in short-term incubations. Laboratory incubations are conducted under artificial temperature and moisture conditions, and thus often are referred to as potential production rates of gaseous C. Field fluxes of CO_2 measured in dark chambers include contributions from both autotrophic and heterotrophic (aerobic and anaerobic) respiration, while CH_4 field fluxes represent the balance between anaerobic production by methanogenic bacteria and oxidation by methanotrophic bacteria (Figure 1-1). By comparing the potential production rates of CO_2 and CH_4 in the laboratory to field-based CO_2 and CH_4 fluxes, I hoped to gain an understanding of autotrophic and heterotrophic respiration responses to permafrost thaw. I did not aim to capture the full extent of variability in decomposition rates over

a growing season. Instead, I sampled in adjacent peatland features (internal lawn, frost mound, and bog) simultaneously to determine the influence of permafrost and permafrost melt on C gaseous production and emission.

Methods

My study area is a peatland complex near Patuanak, Saskatchewan (55°51' N, 107°41' W) situated in the LPZ (Figure 1-2). Ombrotrophic bog, dominated by *P. mariana*, *Ledum groendlandicum*, and *Sphagnum fuscum*, is the most common wetland feature in the area. Also present are isolated frost mounds and internal lawns. The latter represent recent past and/or ongoing permafrost melt. Bogs underlain by permafrost have closed canopies of *P. mariana*; moss cover typically consists of *Pleurozium schreberi* and *Hylocomium splendens*. Internal lawns of western Canada are characterized by *S. riparium, S. angustifolium*, and *Carex* spp.

Using arial photography to locate internal lawns, I established three study sites that each consisted of a frost mound, internal lawn, and continental bog (Figure 1-3). Sites were sampled three times throughout the growing season of 1998 (referred to as 8/98, 9/98, 10/98). In the spring of 1999, a wildfire burned through Site 1, causing considerable melting of the local permafrost lens and extensive damage through the creation of a fire-break (Turetsky and Wieder 2001). I did not sample this site in 1999, but continued to quantify C emissions on four sampling dates (referred to as 7/99, 8/99, 9/99, 10/99) in the two unburned sites.

Potential C production

On each sampling date described above, I collected three replicate wet peat samples from the surface (5-10 cm beneath the moss surface) and at depth (approximately 60-80 cm from the moss surface or directly above the permafrost table) within each peatland feature (internal lawns, bogs, frost mounds). Samples were transported within 48 hours cold to the University of Alberta in plastic bags with air removed from each bag's headspace.

I incubated 10 g subsamples of wet peat at room temperature to determine potential rates of CO_2 and CH_4 mineralization. Samples were incubated in 125 mL Mason jars with rubber septa inserted through lids. Aerobic subsamples were incubated in room air headspace. For anaerobic subsamples, I removed air within mason jars using a vacuum pump and replaced the headspace with O_2-free N_2, repeating this procedure five times to establish anoxic conditions. Stopcock grease was used around lids and septa to prevent headspace leakage. I removed 15 mL of headspace gas with plastic syringes equipped with 3-way Luer-lock stopcocks at 0, 4, 12, 24 and 48 hrs after mason jars were sealed. Gas samples were replaced with equal volumes of room air and N_2 in the aerobic and anaerobic incubations, respectively. Following the incubation, headspace volume within each jar was estimated from the weight of water required to fill each jar to capacity. Samples were then dried at 70 °C until a constant mass to estimate dry mass of the peat.

Peatland field fluxes

Fluxes of CO_2 and CH_4 were quantified in each site using opaque closed chambers (100 l, 0.2 m^2 area) fitted with rubber septa for headspace sampling. On

each sampling date, the three peatland features (frost mound, internal lawn, and continental bog) within a site were sampled simultaneously at midday. Five replicate chambers with sharp plastic edges were placed randomly on each peatland surface and inserted into the peat to a depth of about 5-8 cm. I attempted to minimise installation disturbance by cutting into the peat surface 15-30 min prior to final chamber placement and using temporary boardwalks during sampling in wet areas. Both vascular shrub and non-vascular communities were well represented within chambers, although the chamber volume used necessitated the exclusion of larger shrubs and trees. I used syringes equipped with 3-way Luer-lock stopcocks to mix headspace gas within the chamber prior to collecting 15 ml of headspace gas at 0, 15, 30 and 45 min following the start of the measurement period. At each chamber during the measurement period, I recorded air temperatures near the peat surface and peat temperature at 5 cm depth. Afterwards, water table position relative to the peat surface was measured at several locations throughout the area of chamber placement. Syringes were transported back to the University of Alberta and processed within 48 h.

Gas chromatography

Gas samples were analyzed on a Hewlett Packard 5890 Series II chromatograph using a Chromosorb 102 column and purified He as a carrier gas. Flame ionization and thermal conductivity detectors were used to quantify CH_4 and CO_2 concentrations, respectively. I used external standards of CH_4 (0.5, 1, and 5 ppm) and CO_2 (500, 1000, and 10,000 ppm in helium; Scott Gases, Plumsteadville, PA) for calibration, with standard error of multiple injections < 5%. Flux rates were

calculated from the slopes of headspace (within chamber or mason jar) gas concentration regressed with time. Corrections were made for the N_2 or room air dilutions during laboratory incubations. Nonlinear regressions with R^2 values < 0.95 due to disturbance or ebullition were rejected; data for these chambers are not included in my analysis (approximately 10% of both field fluxes and potential production rates).

Statistical analysis

I used a randomized complete block design, and potential rates of C production were analyzed using a four-way analysis of variance with site as the block effect, peatland feature (internal lawns, bogs, and frost mounds) and oxicity (aerobic vs. anaerobic incubations) as fixed effects, and date (7 sampling dates) and depth (surface vs. deep peat) as random effects (Table 3-1). Variation among replicate incubation jars represents the residual or error term in the ANOVA (Underwood 1997). The feature×date×oxicity×depth mean square term was used to calculate the *F* statistic for the fixed effects, while the error mean square terms were used to calculate other *F* statistics (Underwood 1997). *Post hoc* comparisons of means were accomplished using Tukey's Honestly Significant Difference tests (SAS 1998). All production rates are shown as means ± standard error, expressed in μmol $C_{(g)}$ g dry mass^{-1} d^{-1}. Stepwise multiple regressions were used to determine the influence of peat moisture content on potential production rates.

Peatland field CO_2 and CH_4 fluxes were analyzed with site (site 1, 2, 3) as the block effect, peatland feature (bog, frost mound, internal lawn) as a fixed effect, and

date as a random effect (Table 3-2). Variation among individual chambers, placed randomly on each peatland feature within each site during each sampling date represent the residual or error term in the ANOVA (Underwood 1997). The feature × date mean square term was used to calculate the *F* statistic for the fixed feature effect; error mean square terms were used to calculate other *F* statistics (Underwood 1997). Residuals obtained subsequent to running the ANOVA were not normally distributed, for both CO_2 (Shapiro-Wilk, W=0.3373; p<0.0001) and CH_4 (Shapiro-Wilk, W=0.8076; p<0.0001). Therefore, I report results from an ANOVA run on rank-transformed data. Subsequent to obtaining a significant effect, *a posteriori* comparisons of rank means were accomplished using Tukey's Honestly Significant Difference (THSD) and Unbalanced Design tests (TUB) (SAS 1998).

Stepwise multiple regressions were used to determine the influence of peat temperature, air temperature, and water level height on both CO_2 and CH_4 field respiration. I used a Spearman's correlation test to determine whether CO_2 and CH_4 fluxes were correlated, and Pearson's Correlation tests to investigate correlation between soil temperatures, air temperatures and water table height (SAS 1998). Carbon emissions are shown as means ± standard error, expressed in mmol CO_2 m^{-2} d^{-1} and μmol CH_4 m^{-2} d^{-1}.

Results

Potential C production

Rates of CO_2 production under laboratory conditions varied by 1) peatland feature, 2) oxicity, and 3) depth × sampling date, with no other interactions among

main effects (Table 3-1). Averaged across all peat samples, aerobic incubations produced more CO_2 than did anaerobic incubations, averaging 28.07 ± 1.60 μmol CO_2 g dry wt^{-1} d^{-1} and 22.94 ± 1.40 μmol CO_2 g dry wt^{-1} d^{-1}, respectively (Table 3-1; n=250). Generally, internal lawn peat respired more CO_2 than the other peat types, with production rates almost 2-fold higher than frost mound peat (Figure 3-1). Production rates differ among sampling dates, however, surface peat from the various peatland types produced more CO_2 during aerobic and anaerobic incubations than deep peat (Figure 3-2). Production rates averaged 37.31 ± 2.15 and 43.19 ± 2.05 μmol CO_2 g dry wt^{-1} d^{-1} for 1998 and 1999 sampling dates respectively. Over both growing seasons, approximately 90% of peat samples neither produced nor consumed significant amounts of CH_4, suggesting that the contribution of CH_4 to the overall decomposition at my sites is small. Due to low sample sizes, potential production rates of CH_4 are not reported here.

In all peat types, moisture content was a weak predictor of potential CO_2 production (model $R^2 = 0.05$; $p = 0.0008$). Also, stepwise multiple regressions within each peat type showed that moisture content was only a weak predictor of CO_2 production in internal lawn (model $R^2 = 0.23$; $p = 0.0001$) and frost mound (model $R^2 = 0.08$; $p = 0.0104$) peat, and was not a significant predictor of potential CO_2 production in bog peat (model $R^2 = 0.02$; $p = 0.0976$).

Peatland field fluxes

CO_2 fluxes varied by feature and sampling date, with no significant interaction between these main effects (Table 3-2). Internal lawns had higher CO_2 fluxes (2.59 ±

0.34 mmol CO_2 m^{-2} d^{-1}) than either frost mounds (1.62 ± 0.29 mmol CO_2 m^{-2} d^{-1}) or bogs (1.94 ± 0.31 mmol CO_2 m^{-2} d^{-1}; Table 3-3). In all peatland types, CO_2 fluxes generally were higher in 1998 sampling events than in 1999 (Table 3-3; means ± s.e. for 1998 and 1999 of 2.44 ± 0.27 and 0.80 ± 0.14 mmol CO_2 m^{-2} d^{-1}, respectively).

CH_4 fluxes varied by a feature × sampling date interaction (Table 3-2). In 1998, fluxes were greater from internal lawns than from frost mounds; fluxes from bogs were intermediate and not different from fluxes from either internal lawns or frost mounds (Table 3-3). In contrast, 1999 fluxes from internal lawns were lower than in 1998, and there were no statistically significant differences between features.

Peat temperature and air temperature were positively correlated throughout the 2-yr sampling period (Pearson's correlation coefficient, $r = 0.81$, p=0.0001). While water table levels and peat temperatures showed no correlation ($r = 0.09$, $p = 0.1381$), water table levels were weakly negatively correlated with air temperatures ($r = -0.12$, $p = 0.0580$).

Fluxes of CO_2 and CH_4 were positively correlated (Spearman's correlation coefficient = 0.47, $p = 0.0001$). Stepwise multiple regressions showed that both air and surface peat temperatures, but not water table position (Figure 3-3), were significant predictors of CO_2 emissions (model $R^2 = 0.27$; air temperature, $p < 0.0001$; peat temperature, $p = 0.0026$). Water table level and peat temperature, but not air temperature, were significant, but surprisingly weak predictors of CH_4 flux (model $R^2 = 0.18$; water level, $p < 0.0001$; peat temperature, $p = 0.0084$).

Discussion

Potential C production

Gaseous carbon production rates quantified through laboratory incubations of soil or peat represent heterotrophic respiration from a given mass of peat, with potential contributions also from autotrophic root respiration in near surface samples. Direct comparison between studies investigating potential C production is difficult due to differing laboratory conditions during incubation trials, as rates of peat decomposition vary with degree of decomposition, temperature and water content (cf. Scanlon and Moore 2000). However, rates of CO_2 production measured here generally agree well with published estimates from boreal peats. Previous estimates of CO_2 production range from 0.045 – 113 μmol CO_2 g^{-1} d^{-1} (cf. Waddington *et al.* 2001; Scanlon and Moore 2000; Moore and Dalva 1997), while production rates from my peat samples ranged from 0 – 162.0 μmol CO_2 g dry wt^{-1} d^{-1}.

From a variety of northern peat types, Moore and Dalva (1997) measured average CO_2 production rates in the laboratory of 22.7 and 11.4 μmol CO_2 g^{-1} d^{-1} under aerobic and anaerobic conditions, respectively. While rates of aerobic mineralization from my sites agree well with their data (averaging 28.1 μmol CO_2 g^{-1} d^{-1}), my estimates of anaerobic production (averaging 22.9 μmol CO_2 g^{-1} d^{-1}) are higher than reported estimates. Ratios of aerobic:anaerobic CO_2 production have averaged between 7:1 and 2.5:1.0 (Scanlon and Moore 2000; Bergman *et al.* 1999; Moore and Dalva 1997). Here, aerobic:anaerobic ratios for CO_2 production in frost mound, internal lawn, and bog peat all averaged 1.2:1.0. Relatively low water

contents in my peat samples caused by dry field conditions (Figure 3-3) may explain the high anaerobic CO_2 production rates observed here (Moore *et al.* 2002).

Laboratory incubations of peat collected at various field depths allow for an assessment of where CO_2 tends to be produced throughout a peat profile. Across the three peatland types, peat collected just beneath the vegetation surface showed greater CO_2 production than samples collected from deeper peat layers (Figure 3-2). Higher microbial respiration in surface peat probably is due to larger microbial populations and higher concentrations of nutrients and labile substrates in younger peat. However, root respiration in surface peat samples also may have contributed to greater rates of mineralization in these short-term (2 day) incubations. Averaged across both surface and deep peat, internal lawn samples consistently produced more CO_2 than bog or frost mound peat (Table 3-3; Figure 3-1).

Peatland field fluxes

CO_2 flux measurements using dark static chambers include respiration from living aboveground and belowground plant parts (mosses, sedges, short-statured shrubs) as well as aerobic and anaerobic microbial activity within the peat column (Figure 1-1). They allow for an assessment of C fluxes across the peat surface/atmosphere boundary. Generally, my values for CO_2 flux (mean ± s.e. = 2.05 ± 0.18 mmol CO_2 m^{-2} d^{-1} across 170 chambers) agree with other studies using static chambers to quantify CO_2 flux from peatlands. For example, emissions averaged 1.20 and 3.95 mmol CO_2 m^{-2} d^{-1} for a bog and poor fen in Alberta, respectively (Vitt *et al.* 1990). Moore and Knowles (1987) reported rates of CO_2 evolution from subarctic

fens in Quebec ranging from 2.00-29.00 mmol CO_2 m^{-2} d^{-1}, while fluxes measured in drained swamp peatlands in southern Quebec ranged from 0-0.36 mmol CO_2 m^{-2} d^{-1} (Shannon *et al.* 1993).

Methane fluxes from peatlands typically show large variation, both temporally and spatially (Waddington and Roulet 1996; Van den Pol-Van Dasselaar *et al.* 1999; Kettunen *et al.* 2000). Methane flux from my peatland sites ranged from -24.2 - 344.4 μmol CH_4 m^{-2} d^{-1}, and averaged 6.4 ±2.1 μmol CH_4 m^{-2} d^{-1} (across 178 chamber measurements). These flux estimates are low compared to other published values. Few studies, however, have investigated CH_4 flux from western continental peatlands where conditions tend to be dry with low water tables (but see Suyker *et al.* 1996). Vitt et al. (1990) also used static chambers to quantify CH_4 emissions from peatlands in northern Alberta, and measured negligible CH_4 emissions from a bog, and mean rates of 56.3 μmol CH_4 m^{-2} d^{-1} from a poor fen. Episodic rain events may play important roles in controlling pulses of CH_4 emissions from these moisture deficient peatlands (Kettunen *et al.* 2000). This process is difficult to characterize in a remote field setting. More temporally intensive measurements of CH_4 emissions in peatlands affected by permafrost melt are needed.

Controls on peat decomposition

Both field and laboratory approaches have identified soil temperatures and water table position as important environmental controls on C mineralization to CO_2 in organic soils (Scanlon and Moore 2000). In this study, peat moisture content during laboratory incubations was a weak predictor for CO_2 production, explaining between 0

(bog) – 23 (internal lawn) % of variation in decomposition among the three peat types. Peat and air temperatures during chamber measurements (Figure 3-3) together explained only about 25 % of the variation in CO_2 field fluxes, and showed significant co-linearity. Additionally, heights of water (bogs and internal lawns) or permafrost (frost mounds; Figure 3-3) tables were not important controls on field CO_2 fluxes in these boreal peatlands. Water level measurements in our sites were correlated with air temperatures, yet neither were important predictors of CH_4 flux.

Carbon balance

Both laboratory incubations and field-based flux measurements show higher rates of CO_2 respiration in internal lawns than in unfrozen bogs or frost mounds. Root biomass and respiration is relatively small in peatlands compared to uplands (Bhardwaj 1997), therefore, it seems likely that the observed patterns in decomposition are due to increased heterotrophic CO_2 respiration following permafrost melt. The conversion of frost mounds to internal lawns is associated with a 1.9-fold increase in CO_2 production under laboratory conditions (Figure 3-1) and a 1.6-fold increase in CO_2 flux across the peatland/atmosphere boundary (Table 3-3).

Laboratory incubations suggest that CH_4 production by microbes does not contribute significantly to the overall patterns of decomposition in these boreal peat types. Field flux measurements also show low rates of CH_4 emissions from internal lawns, bogs, and frost mounds, with an average ratio of CO_2:CH_4 emission of 324:1. Methanogens are extremely sensitive to oxygen-rich environments, often showing no signs of CH_4 production even when returned to anoxic conditions (Whalen and

Reeburgh 2000). However, Oquist and Sundh (1998) found that methanogens in surface peat remained viable after several weeks of oxic conditions while microorganisms in deeper peat layers were rendered inactive. Here, neither surface nor deep peat samples produced CH_4 at rates significantly different from zero. Ombrotrophic peatlands in continental Canada typically have water tables lower than 30-40 cm beneath the moss surface (Figure 3-3). It seems likely that methanogenesis in western peatlands is limited solely to deeper peat deposits underneath the highly fluctuating water tables (Figure 3-3) driven by continental climate regimes. Low water tables probably contribute to minimal CH_4 flux to the atmosphere, as CH_4 produced at depth is oxidized as it diffuses upward through thick aerobic surface peat layers (Figure 1-1). Although water tables in our sites were slightly higher in 1999 than in 1998, particularly within frost mounds (Figure 3-3), they were not high enough to significantly enhance CH_4 emission relative to 1998.

The melting of permafrost creates wet peatland features interspersed within a relatively dry landscape. Internal lawns are associated with higher rates of CH_4 emissions across the peat surface/atmosphere boundary compared to bogs or frost mounds. My results suggest that permafrost thaw is associated with 30-fold increases in CH_4 emissions to the atmosphere.

Peat accumulation represents the balance between net primary production (NPP) and gaseous C losses from heterotrophic respiration plus dissolved C losses (Figure 1-1). Previous work has shown that internal lawns accumulate near-surface peat at rates 40% greater than in bogs or frost mounds over the past 100 yr (Turetsky *et al.* 2000; Camill *et al.* 2001; Chapter 2). Here, we show that the conversion of frost

mounds to internal lawns also is associated with increases in both CO_2 and CH_4 emissions to the atmosphere. Increases in both peat accumulation and heterotrophic respiration suggests that internal lawn NPP also must be higher compared to NPP in frost mounds, from which internal lawns are derived.

While frost mounds may remove CH_4 from the atmosphere through oxidation, internal lawns showed high net CH_4 flux to the atmosphere in our sampling over two frost-free seasons. As CH_4 has greater greenhouse warming potential relative to CO_2 (Schimel *et al.* 1996), continued permafrost melt on a regional scale in the LPZ of boreal western Canada may represent a positive feedback on climate change. Although internal lawns will undergo succession, eventually to continental bogs (Camill 1999; Turetsky *et al.* 2000; Chapter 2), the temporal trajectory of this development is poorly known.

Different permafrost regimes appear to influence CH_4 and CO_2 fluxes across the peatland/atmosphere boundary, and therefore the patchy spatial distribution of peatland features (bogs without permafrost, frost mounds, and internal lawns representing recent thaw) should be considered when scaling-up from site-specific studies to estimate boreal peatland C budgets to regional scales.

Table 3-1. Results of a four-way analysis of variance for potential production rates of CO_2, with site as a blocked effect, date and depth as random effects, and feature and aerobic as fixed effects. The error mean square term is equivalent to variation among replicate incubation jars for each site×feature×date×depth×aerobic combination. The feature×date×depth×aerobic mean square term is used to calculate the *F* statistic for the fixed feature effects; error mean square terms are used to calculate other *F* statistics (Underwood 1997).

Model Effects	df	Type III Sum of Squares	*F*	*p*
Site	2	817.55	1.31	0.2705
Feature	2	7824.93*	22.26	0.0002
Date	6	10485.97	5.61	0.0001
Depth	1	60283.46	193.44	0.0001
Aerobic	1	2895.48*	16.47	0.0023
Feature*Date	12	3687.73	0.99	0.4612
Feature*Depth	2	887.95	1.42	0.2418
Feature*Aerobic	2	204.39	0.33	0.7206
Date*Depth	6	7444.26	3.98	0.0007
Date*Aerobic	6	830.52	0.44	0.8491
Depth*Aerobic	1	495.26	1.59	0.2081
Feature*Date*Depth	11	1815.97	0.53	0.8832
Feature*Date*Aerobic	12	1953.85	0.52	0.9004
Feature*Depth*Aerobic	2	62.16	0.10	0.9051
Date*Depth*Aerobic	6	1807.60	0.97	0.4474
Feature*Date*Depth*Aerobic	10	1757.54	0.56	0.8433
Error	416	129639.27		

*feature×date×depth×aerobic mean square used to calculate *F* statistic

Table 3-2. Analysis of variance results conducted on ranks of C emission data, with site as a blocked effect, feature as a fixed effect and date as a random effect. The error mean square term is equivalent to variation among chambers for each site×feature×date combination. The feature×date mean square term is used to calculate the *F* statistic for the fixed feature effect; error mean square terms are used to calculate other *F* statistics (Underwood 1997).

CO_2 Model Effects	**df**	**Type III Sum of Squares**	***F***	***p***
Site	2	2188	0.71	0.4950
Feature	2	17437	3.84*	0.0513
Date	6	99961	10.76	<0.0001
Feature×Date	12	27233	1.47	0.1475
Error	146	226081		
CH_4 Model Effects				
Site	2	10267	3.69	0.0271
Feature	2	93781	12.04*	0.0014
Date	6	47630	5.71	<0.0001
Feature×Date	12	46721	2.80	0.0017
Error	155	215402		

*Feature×Date mean square used to calculate *F* statistic

Table 3-3. Mean (s.e.) CO_2 and CH_4 fluxes from adjacent bogs, internal lawns (recent permafrost thaw), and frost mounds (intact permafrost) in north-eastern Saskatchewan on seven sampling dates. For CO_2, different superscript letters or numbers denote significant *a posteriori* differences between dates or features, respectively (Tukey's HSD). For CH_4, different letter superscripts denote significant *a posteriori* differences between feature×date means.

	CO_2 flux (mmol m^{-2} d^{-1})			CH_4 flux (μmol CH_4 m^{-2} d^{-1})		
Date	**Bogs[2]**	**Internal lawns[1]**	**Frost mounds[2]**	**Bogs**	**Internal lawns**	**Frost mounds**
8/98	3.40 (0.35)^{a}	4.44 (0.54)^{a}	2.25 (0.41)^{a}	6.26 (2.20)$^{a-c}$	26.18 (5.76)^{a}	0.26 (0.71)^{de}
9/98	2.89 (1.16)^{b}	1.38 (0.25)^{b}	1.66 (0.55)^{b}	3.64 (2.10)$^{b-e}$	9.18 (2.63)$^{a-c}$	0.28 (0.99)^{de}
10/98	2.01 (0.94)^{b}	3.39 (1.12)^{b}	2.49 (1.30)^{b}	2.64 (0.55)$^{a-e}$	38.27 (28.03)^{ab}	-1.20 (0.69)^{e}
7/99	0.78 (0.27)^{bc}	2.00 (0.43)^{bc}	0.29 (0.08)^{bc}	-0.11 (0.32)^{de}	0.56 (0.75)^{de}	0.04 (0.35)^{de}
8/99	0.82 (0.27)^{bc}	3.17 (2.19)^{bc}	0.72 (0.23)^{bc}	-0.40 (0.44)^{de}	1.50 (1.72)$^{b-e}$	-0.68 (0.83)^{e}
9/99	0.86 (0.18)^{bc}	1.55 (0.67)^{bc}	1.45 (0.52)^{bc}	3.76 (1.23)$^{a-d}$	3.94 (2.80)$^{b-e}$	0.71 (8.16)$^{c-e}$
10/99	0.38 (0.07)^{c}	0.42 (0.15)^{c}	0.59 (0.11)^{c}	0.69 (0.15)$^{c-e}$	3.48 (1.26)$^{a-e}$	0.002 (0.19)^{de}

Figure 3-1. CO_2 production rates (mean ± s.e.) averaged across sampling dates and depth of collection for internal lawns (IL), continental bogs (CB), and frost mounds (FM) situated in central Saskatchewan. Means with same letter superscripts do not differ from one another (Table 3-1; n = 252 incubations).

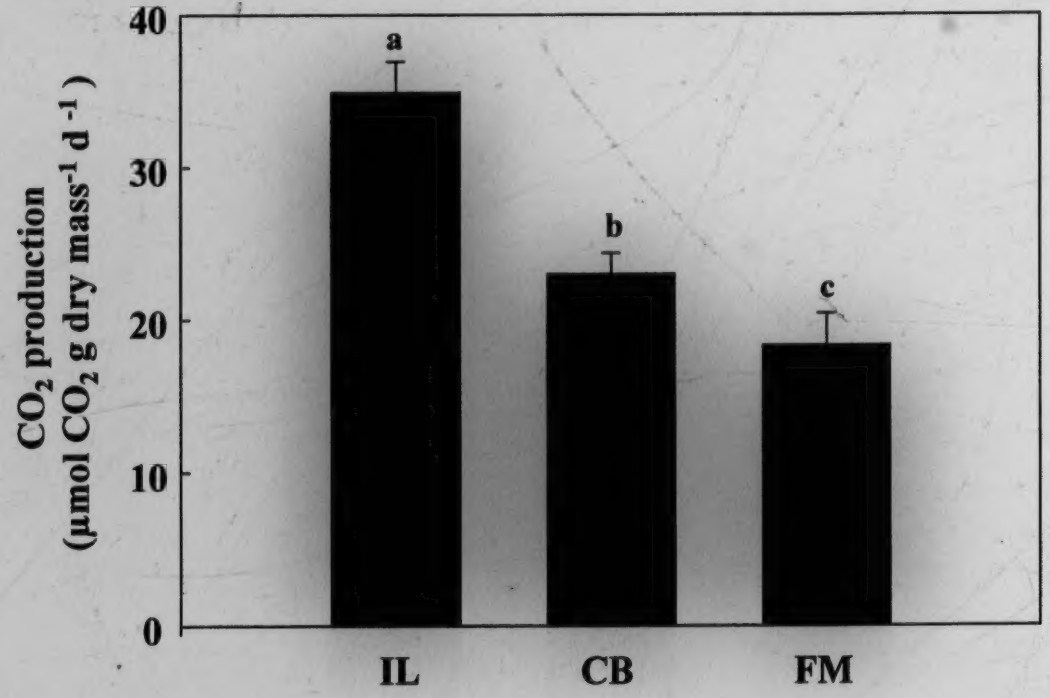


Figure 3-2. Mean CO_2 production rates averaged across the three peatland types for surface and deep peat collected on 7 sampling dates in 1998 and 1999. Means with same letter superscripts do not differ from one another (Table 3-1; n=54 for 1998 sampling dates and 36 for 1999 post-fire sampling dates).

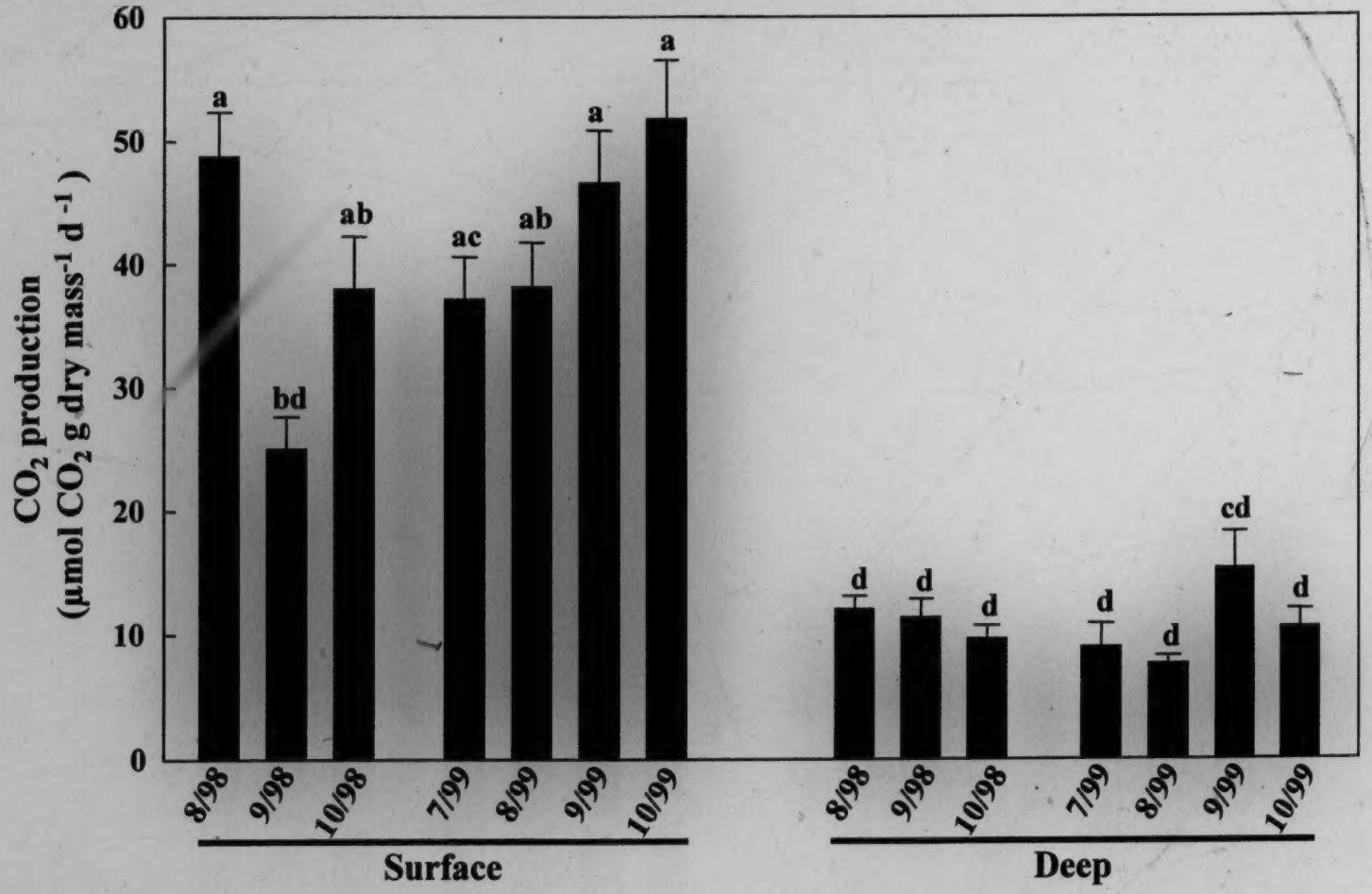


Figure 3-3. Mean surface peat temperatures, air temperatures, and water table position (± s.e.; n=15 and 10 in 1998 and 1999, respectively) in continental bogs, internal lawns, and frost mounds during the 1998 and 1999 sampling events. In frost mounds, we measured depth to the permafrost table or active layer (*i.e.*, seasonally melting ice lying above the permafrost table). Water tables at 0 cm would be flush with the moss surface.

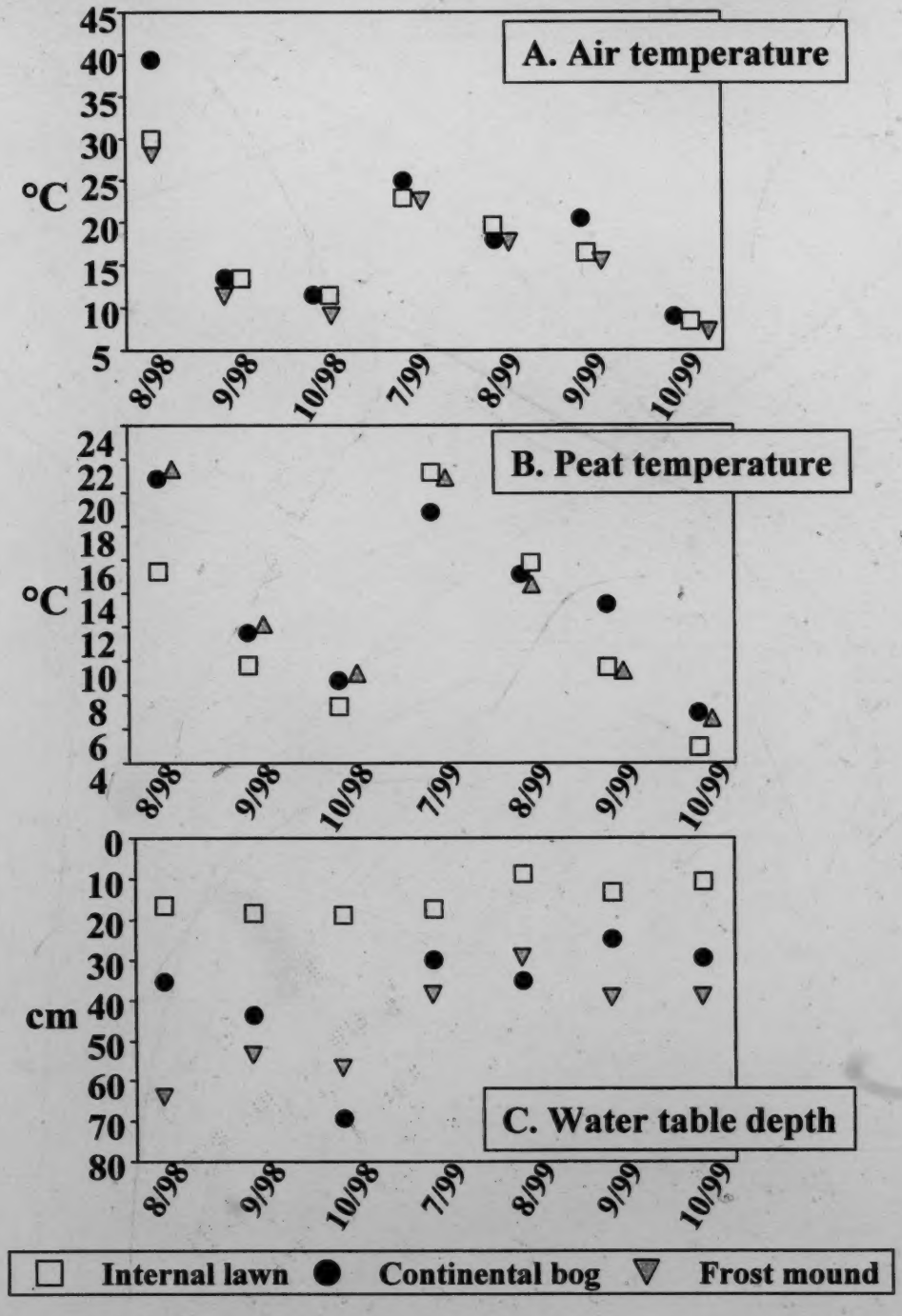
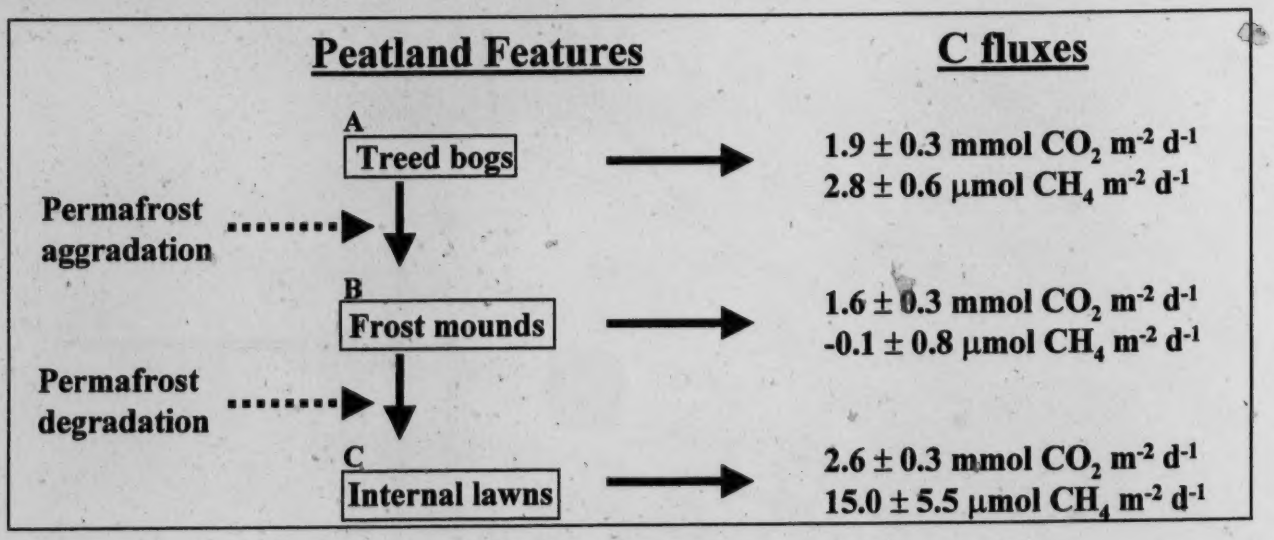


Figure 3-4. Schematic of peatland development (Figure 2-5) and carbon gaseous emissions within discontinuous permafrost in western Canada. **A**) Carbon dioxide fluxes were much greater than CH_4 fluxes from the unfrozen bogs. Our estimates of CH_4 flux are low compared to previous estimates from boreal bogs. **B**) Permafrost aggradation elevates soil surfaces above the surrounding landscape, as permafrost formation causes volume expansion of freezing soil water. Carbon dioxide fluxes from isolated frost mounds are similar to emissions from bogs. However, unlike the other peatland features, which acted as net methane sources, frost mounds occasionally showed net consumption of CH_4 from the atmosphere. **C**). Permafrost in peatlands recently has been melting across western Canada, creating wet *Sphagnum-Carex* lawns (internal lawns) interspersed within drier ombrotrophic bog. Internal lawns in my study area are associated with 1.6- and 30-fold greater CO_2 and CH_4 emissions, respectively compared to nearby peatland types. This suggests that permafrost melt stimulates microbial activity in peat (Figure 1-1), thereby increasing emission rates of gaseous decay products to the atmosphere.



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Chapter 4. Bryophyte Chemistry and Decomposition in Boreal Peatlands

Introduction

Peatlands are saturated areas where the production of plant biomass exceeds rates of microbial decomposition (Vitt *et al.* 2001, Frolking *et al.* 1998). Covering only 3 - 5 % of the world's ice-free land area, peatlands store about 33 % of global terrestrial soil carbon (Gorham 1991) and represent a long-term sink of atmospheric CO_2. Peatlands are widespread in northern regions where cool climatic conditions limit decomposition. Generally, organic matter decomposition is regulated by climate, the physical properties of litter, and decomposer communities. High moisture content (Scanlon and Moore 2000), low soil temperature (Waddington *et al.* 2001), and poor litter quality (Yavitt *et al.* 2000, Verhoeven and Liefveld 1997, Updegraff *et al.* 1995, Valentine *et al.* 1994) have been identified as important decay controls. Nonvascular species such as *Sphagnum* mosses tend to decay more slowly than vascular plants (Aerts *et al.* 1999). However, decomposition rates can differ more among individual *Sphagnum* species than between microhabitats (Johnson and Damman 1991, Rochefort *et al.* 1990).

To provide further insight into the influence of moss species on peatland decomposition, I present initial results from a reciprocal transplant experiment evaluating the decay of 8 moss species (*Sphagnum angustifolium, S. fuscum, S. jensenii, S. magellanicum, S. riparium, Pleurozium schreberi, Scorpidium scorpioides, Tomenthypnum nitens*) within several peatland environments, including a bog, poor fen,

extreme rich fen, and a frost mound with active thermokarst pools. My goals were to: 1) determine whether decomposition rates are controlled by species, peatland type, and/or microhabitat, 2) relate observed patterns of decomposition to organic matter quality (i.e. concentrations of labile and recalcitrant compounds).

Site descriptions

Based on site accessibility, I selected four peatland sites from which bryophytes were harvested and into which our samples were reciprocally transplanted (Figure 1-4). Precipitation and temperature data are derived from the nearest climate station and averaged over the period between 1960-1990.

Rich fen (52° 50 'N, 116° 51 'W): a wet open extreme-rich marl fen located in Alberta's Rocky Mountain foothills region. Vegetation includes a sparse *Larix laricina* cover, large hollows dominated by *Scorpidium scorpioides*, hummocks of *Tomenthypnum nitens* and *S. warnstorfii,* and lawns of *Drepanocladus revolvens*. Surface water pH is 7.6. Annual temperature and precipitation average 1.0 °C and 596 cm (Environment Canada 1998).

Poor fen (55° 32.2 'N, 112° 20 'W): an acidic, weakly patterned poor fen in the Continental High Boreal Wetland Region (Zoltai 1988) with mean annual temperature and precipitation of 0.8 °C and 462.7 mm (Environment Canada 1998). *Sphagnum magellanicum* and *S. angustifolium* are dominant in hummocks while *S. jensenii* is

common in large hollows. Surface water pH is 4.2. The water table is less than 10 cm from the vegetation surface in hummocks, and lies flush with the moss layer in hollows.

The bog and frost mound sites are located outside of Anzac, Alberta in the Continental High Boreal Wetland Region (Zoltai 1988). Mean annual temperature is 0.2 °C and annual precipitation averages 465 mm (1944-1990 climate normals, Environment Canada 1998).

Bog (56° 28.3 'N, 111° 2.5 'W): an ombrotrophic, *Sphagnum*-dominated bog with a water table approximately 65-80 cm below the peat surface. *Sphagnum fuscum* and *S. angustifolium* are the dominant hummock and hollow species, respectively, while *S. magellanicum* is common at mid-hummocks. The pH of surface water is 4.6.

Frost mound (56° 28.4 'N, 111° 2.5 'W): is dominated by a dense stand of *P. mariana*, while groundcover is dominated by *Pleurozium schreberi*, *Hylocomium splendens* and *Cladina* spp. The permafrost table is 50-60 cm in depth below the peat surface, with little water associated with the active layer throughout the growing season. There is active permafrost degradation in this site that creates internal and lateral pools dominated by *S. riparium* and *S. angustifolium*. Surface water pH of thaw pools ranges from 4.3 to 4.5.

Methods

Organic Mass Loss

During the growing season of 1999, I harvested stands of eight bryophyte species, including one hummock and one hollow species typical of continental bogs, poor fens, rich fens, and frost mounds (Figure 1-4). Mosses were sorted into individual plants, cleaned of debris and fine roots, and cut into sections of 0-5 cm (brown mosses) or 1-5 cm (excluding developing leaves within *Sphagnum* capitula that tend to have high bulk density and nutrient concentrations). I dried plant sections at 70 °C for ~48 hr to a constant mass before filling plastic storage tubes (10 cm × 4 cm) with approximately 2 g dry weight of a single moss species. Sample masses were recorded and tubes were sealed with perforated plastic end caps lined with nylon mesh. For each species, I analyzed triplicate subsamples of moss material for organic matter quality (methods below).

In September of 1999, 10 tubes of each species (hereafter referred to as peat traps, cf. Wieder and Yavitt 1991) were reciprocally transplanted into multiple hummocks and hollows of every peatland type (bog, frost-thaw, rich fen, poor fen). Peat traps were buried at a depth of 10 cm from the vegetation surface. Samples were incubated *in situ* for one year, after which three replicates were collected from each species × topography × peatland type combination. I dried samples in the laboratory at 70 °C for ~ 48 hours to a constant mass. Sample weights were recorded before and after drying to calculate water content. I removed any root growth with forceps before dried samples were weighed and homegenized. For each peat trap, I quantified ash concentrations using loss on ignition for 4 hr at 550 °C, and organic matter quality (methods below).

Decomposition rates are expressed as the loss of ash-free, dry organic matter (mg of organic matter lost per gram of initial organic matter) over the 1-yr incubation period. I analyzed decomposition rates within each peatland type using two-way analyses of variance and performed *post hoc* mean comparisons using Tukey tests (SAS 1998). All values are presented as means ± standard errors.

Organic Matter Quality

I used sequential extractions to separate the following fractions: soluble nonpolars (lipids such as fats, oils, and waxes), water-soluble carbohydrates, hot-water-soluble phenolics, holocellulose (complex carbohydrates), and acid-insoluble material (tannins, lignin, and polyphenols) (Wieder and Starr 1998). These five organic fractions previously have been isolated in bulk *Sphagnum* peat (Wieder and Starr 1998) and have different functions in plant material. Water-soluble carbohydrates are simple carbohydrates such as glucose, sucrose, and fructose. These sugars are early products of photosynthesis and are readily metabolized (Van Cleve and Powers 1995). The soluble nonpolar fraction, comprised of fats, oils, and waxes, also serves as a good energy source, with high energy yields through the metabolic breakdown of their C-C bonds. Cellulose, a glucose polymer with 1-4 linkages between adjacent molecules, is a structural carbohydrate important in plant cell walls. Cellulose decomposition is slow in peatlands (Santelmann 1992), but can be broken down by cellulase, an extracellular enzyme produced by bacteria and fungi. Cellulase depolymerizes cellulose to cellobiose which is then hydrolyzed to glucose (Van Cleve and Powers 1995). The acid insoluble fraction is comprised largely of tannins, cutins, and lignin (Preston et al. 1997). Lignin is comprised

of phenylpropane units found in association with the cell walls of vascular plants. While bryophytes are not capable of synthesizing lignin, other phenolic compounds such as p-hydroxyphenyl networks, p-coumaric acid, and sphagnum acid have been quantified in *Sphagnum* material (Rasmussen et al. 1995; Williams et al. 1998). Williams *et al.* (1998) concluded that Sphagnum mosses possess a lignin-like polymer with simple monomers linked by simple ether/ester bonds. Phenolic compounds are known to have low metabolic energy yield to soil microbes. Few microorganisms can break down lignins, and it is impermeable to most anaerobic decay processes. Lignin and cellulose often are associated in plant cell wall structures, and add compressional strength and flexibility to plant tissues.

For each organic fraction, I calculated turnover rates (yr^{-1}) as:

((initial mass-final mass) ÷initial mass)÷1 yr

such that gains in organic matter mass during the incubation period yield negative turnover rates. All organic chemistry data are expressed on an ash-free, dry mass basis. I used a stepwise multiple regression to investigate the influence of moss chemistry and peat trap moisture content on decomposition rates (SAS 1998).

Results

Bryophyte decay

Following a one-year, *in situ* incubation, the water content of peat traps ranged from 50-700 mg g^{-1}, averaging 347 ± 11 mg g^{-1} (n= 190, Table 4-1). Organic matter

losses incubated in the rich fen varied significantly among species and topography, with no significant interaction between these main effects (Table 4-2). Mass loss was significantly greater in the hummocks (165.7 ± 16.2 mg g^{-1}, k= 0.18 yr^{-1}) compared to hollows (137.9 ± 16.6 mg g^{-1}, k= 0.15, n=24, Table 4-2). Averaged across hummocks and hollows, rich fen decomposition rates varied among species, ranging from 41 ± 7 mg g^{-1} (k= 0.04 yr^{-1}) for *S. fuscum* to 320 ± 3 mg g^{-1} (k= 0.39 yr^{-1}) for *S. riparium* (Figure 2A).

Organic matter loss in the bog, frost mound, and poor fen varied by a species × topography interaction (Table 4-2, Figure 4-2B-D). Across all peatland sites, however, differences in decay rates among species outweighed differences occurring with microtopography (Figure 4-2). Decay rates did not differ significantly among peatland types (bog: 128 ± 8 mg g^{-1}, k=0.14 yr^{-1}, frost mound: 128 ± 9 mg g^{-1}, k=0.14 yr^{-1}, poor fen: 139 ± 10 mg g^{-1}, k=0.14 yr^{-1}, rich fen: 152 ± 12 mg g^{-1}, k=0.16 yr^{-1}, one way ANOVA: df = 3, F = 1.51, p = 0.2018).

Across both microtopography positions and all peatland types, organic matter losses varied significantly among species (one-way ANOVA: p=<0.0001, F=36.15, 7 df, n=24, SAS 1998): *S. riparium* (271 ± 7 mg g^{-1}, k=0.32 yr^{-1}) > *S. magellanicum* (151 ± 9 mg g^{-1}, k=0.16 yr^{-1}) = *S. jensenii* (133 ± 6 mg g^{-1}, k=0.14 yr^{-1}) = *P. schreberi* (129 ± 5 mg g^{-1}, k=0.14 yr^{-1}) = *S. angustifolium* (127 ± 4 mg g^{-1}, k=0.14 yr^{-1}) > *T. nitens* (100 ± 4 mg g^{-1}, k= 0.11 yr^{-1}) = *S. scorpioides* (94 ± 7 mg g^{-1}, k=0.10 yr^{-1}) > *S. fuscum* (65 ± 5 mg g^{-1}, k=0.07 yr^{-1}).

Bryophyte chemistry

Bryophyte species can be separated by multivariate analysis using concentrations of organic matter fractions (Figure 4-3). In this analysis, *Sphagnum* species were more similar to one another than to the brown mosses (*S. scorpioides, T. nitens, P. schreberi*). *Sphagnum* species had greater concentrations of water-soluble phenolics and holocellulose compared to the other mosses. Moss chemistry was important in predicting subsequent decomposition (Table 4-3). Water-soluble carbohydrates alone explained almost 70 % of the variation in bryophyte decomposition rates, and showed a positive relationship with mean organic matter loss among moss species (Table 4-3, Figure 4-4). Other predictors, such as water content and acid-soluble carbohydrates explained an additional 7 % of variation in decay rates (Table 4-3).

Water-soluble carbohydrates exhibited the fastest turnover rate (Table 4-1), averaging 0.75 ± 0.01 yr^{-1} across all species, peatland types, and microtopography positions. Soluble nonpolars, holocellulose, and water-soluble phenolics had slower turnover rates than soluble carbohydrates, averaging 0.62 ± 0.04, 0.45 ± 0.01, and 0.28 ± 0.02 yr^{-1}, respectively. Acid-insoluble material increased marginally during the 1-yr experiment (Table 4-1), with a slightly negative turnover rate averaging -0.10 ± 0.06 yr^{-1}.

Discussion

Decomposition in peatlands

I evaluated short-term decay rates of moss litter, as 1) peat accumulation in northern regions is dominated by bryophyte remains, 2) decomposition in peatlands occurs primarily in surface peat before transfer to deeper, anoxic layers (Wieder 2001,

Clymo *et al.* 1998), and 3) previous studies have reported substantial mass losses in bryophyte litter during the first 20-45 days, with little mass loss during the following 2 years (Thormann *et al.* 2001, Scheffer *et al.* 2001). Published values of bryophyte or peat mass losses range from 50 – 270 mg g^{-1} y^{-1} (Lieffers 1988, Berg *et al.* 1984, Farrish and Grigal 1988). My values for organic mass losses (ash-free) of bryophytes in boreal peatlands fit well with published estimates, averaging 134.5 ± 46 mg g^{-1} over the 1-yr field incubation.

Previous litter bag studies reported lower decay rates in the hummock species *Sphagnum fuscum and S. capillifolium* than the wet-loving hollow species *S. cuspidatum* and *S. angustifolium* (Rochefort *et al.* 1990, Johnson and Damman 1991, Belyea 1996). Such patterns have been used to explain the maintenance of peatland microtopography, where low lying hollows are maintained by fast decomposition compared to slow decay in drier hummocks. However, these studies have been limited mainly to single peatland sites and have considered only *Sphagnum* decay. Here, I selected common hummock and hollow mosses from four boreal peatland types for this reciprocal transplant design. *Sphagnum fuscum* was the only hummock species that consistently decayed slowly across all sites. The other hummock species, including *P. schreberi, T. nitens,* and *S. magellanicum*, did not decay more slowly than hollow species (*S. scorpioides, S. riparium, S. angustifolium, S. jensenii*).

Sphagnum riparium plants lost almost 30% of their initial organic matter loss during the incubation. This species had higher concentrations of water-soluble carbohydrates than other mosses (Figure 4-4). I suggest that *S. riparium* is divesting

more energy into metabolic compounds than other *Sphagnum* species to sustain fast growth (cf. Pakarinen and Vitt 1974).

Control on bryophyte decay

Scheffer *et al.* (2001) found no difference in vascular and nonvascular plant decomposition within an acidic *Sphagnum*-dominated fen and a fen without *Sphagnum*. Averaged across species and microtopography, my results suggest no significant differences in decomposition rates among acidic or calcareous peatland types. Together, these results suggest that *Sphagnum*-generated acidity does not control short-term organic matter decay.

Water availability, measured here as peat trap water content (Table 4-1), was a weak predictor of bryophyte decomposition, explaining 4% of the total variation in decay rates (Table 4-3). Among all species and peatland types, organic matter losses were 134 ± 6 (k=0.14 yr^{-1}) and 135 ± 7 (k=0.15 yr^{-1}) mg g^{-1} in dry hummocks and wet hollows, respectively.

Slow microbial decay in peatlands also has been attributed *Sphagnum* chemistry, including low N concentrations, high concentrations of phenolics such as sphagnum acid and hydroxybutenolide, organic acid generation, and proton exchange from polyuronic cell wall structures (cf. Tsuneda *et al.* 2001, Williams *et al.* 1998, Verhoeven and Toth 1995). However, I measured greater concentrations of labile compounds, such as water-soluble phenolics, soluble carbohydrates, and holocellulose, in *Sphagnum* material than in the other moss species. Recalcitrant fractions such as acid-insoluble material were not important predictors of decay (Figure 4-4, Table 4-3). Water-soluble carbohydrates,

ranging from 13-125 mg g dry weight^{-1}, explained 70 % of the variation in decomposition rates (Figure 4-4, Table 4-1). These results indicate that mosses vary considerably in their concentration of soluble carbohydrates. These labile compounds are linked to metabolic functions, and appear to serve as important substrates for short-term decay. More recalcitrant fractions such as holocellulose-lignin complexes will become dominant as concentrations of labile compounds diminish (Melillo *et al.* 1989, Berg *et al.* 1984).

Conclusions

Bryophyte mass losses did not reveal consistent patterns of decomposition among peatland types (acidic vs. calcareous) or among hummocks and hollows (dry vs. wet). The xeric, late successional bog moss, *Sphagnum fuscum*, decayed slowly across all peatland types, while *Sphagnum riparium*, a colonizer of recently melted permafrost thaw pools, decomposed 2.4 times faster than other mosses. Peatland mosses differ chemically, with varying amounts of labile and recalcitrant carbon compounds. Concentrations of water-soluble carbohydrates were the most important predictor of decomposition in this study. Shifts in the species composition of peatlands with natural succession or disturbance will impact substrate pools, decay rates and ultimately C storage as peat.

Table 4-1. Water contents, organic fraction concentrations (mg g^{-1} ash-free dry weight) and organic fraction turnover rates (mg g^{-1} dry mass) within each incubation combination of moss species × peatland type × microtopography. Abbreviations as follows: SFOW=Soluble nonpolars, Sol Carbs=water-soluble carbohydrates, Sph ang=*Sphagnum angustifolium*, Sph fus=*S. fuscum*, Sph jen=*S. jensenii*, Sph mag=*S. magellanicum*, Sph rip=*S. riparium*, Sco sco=*Scorpidium scorpioides*, and Tom nit=*Tomenthypnum nitens*.

Species	Transplanted to:	Microtopography	Water content (mg g^{-1})	SFOW (yr^{-1})	Sol Carbs. (yr^{-1})	Acid Insolubles (yr^{-1})	Holo-cellulose (yr^{-1})	Water-soluble phenolics (yr^{-1})
Sph ang	Initial (mg g^{-1})	--	--	46.7 ± 16.3	47.8 ± 14.1	126.8 ± 14.8	651.3 ± 43.9	3.3 ± 0.6
	Bog	Hollow	39.9 ± 3.3	0.9 ± 0.1	0.8 ± 0.1	0.1 ± 0.1	0.5 ± 0.01	0.1 ± 0.1
		Hummock	17.0 ± 3.5	0.7 ± 0.1	0.6 ± 0.04	-0.8 ± 0.7	0.3 ± 0.1	0.3 ± 0.1
	Permafrost	Hollow	45.4 ± 0.3	0.8 ± 0.02	0.5 ± 0.02	-2.6 ± 0.5	0.5 ± 0.03	0.3 ± 0.03
		Hummock	19.4 ± 0.6	0.6 ± 0.04	0.6 ± 0.02	-0.01 ± 0.2	0.4 ± 0.02	0.2 ± 0.04
	Poor Fen	Hollow	47.8 ± 1.6	0.7 ± 0.1	0.7 ± 0.1	-0.9 ± 0.4	0.5 ± 0.1	0.4 ± 0.03
		Hummock	35.8 ± 4.3	0.7 ± 0.04	0.6 ± 0.1	0.2 ± 0.1	0.5 ± 0.03	0.2 ± 0.1
	Rich Fen	Hollow	38.2 ± 1.3	0.4 ± 0.01	0.7 ± 0.01	0.5 ± 0.02	0.5 ± 0.01	0.6 ± 0.01
		Hummock	29.4 ± 2.4	0.5 ± 0.1	0.8 ± 0.02	0.3 ± 0.1	0.5 ± 0.1	0.7 ± 0.03
Sph fus	Initial (mg g^{-1})	--	--	46.0 ±4.1	33.3 ± 3.0	349.5 ± 107.8	641.0 ± 8.4	4.2 ± 0.3
	Bog	Hollow	43.1 ± 3.5	0.7 ± 0.2	0.4 ± 0.1	0.3 ± 0.3	0.5 ± 0.03	0.2 ± 0.1
		Hummock	18.1 ± 2.8	0.8 ± 0.2	0.6 ± 0.1	-0.5 ± 0.4	0.4 ± 0.1	0.4 ± 0.1
	Permafrost	Hollow	47.8 ± 1.0	0.8 ± 0.1	0.4 ± 0.1	-0.6 ± 0.5	0.4 ± 0.1	0.3 ± 0.2
		Hummock	24.2 ± 1.7	0.3 ± 0.1	0.6 ± 0.04	0.3 ± 0.4	0.5 ± 0.01	0.3 ± 0.1
	Poor Fen	Hollow	49.1 ± 1.4	0.6 ± 0.03	0.8 ± 0.1	-0.1 ± 0.2	0.6 ± 0.1	0.4 ± 0.1
		Hummock	44.6 ± 2.7	0.3 ± 0.1	0.5 ± 0.03	0.3 ± 0.1	0.6 ± 0.01	0.3 ± 0.01
	Rich Fen	Hollow	42.1 ± 2.0	0.2 ± 0.1	0.7 ± 0.04	0.4 ± 0.1	0.5 ± 0.04	0.6 ± 0.1
		Hummock	42.0 ± 1.0	0.5 ± 0.2	0.8 ± 0.03	0.5 ± 0.02	0.4 ± 0.03	0.7 ± 0.03
Sph jen	Initial (mg g^{-1})	--	--	41.3 ± 2.9	74.0 ± 11.4	154.1 ± 14.3	655.4 ± 12.8	3.2 ± 0.2
	Bog	Hollow	52.5 ± 2.3	0.6 ± 0.2	0.8 ± 0.01	0.6 ± 0.03	0.5 ± 0.02	0.1 ± 0.1
		Hummock	16.2 ± 5.3	0.9 ± 0.1	0.9 ± 0.01	-0.8 ± 0.6	0.2 ± 0.1	0.3 ± 0.03
	Permafrost	Hollow	56.4 ± 1.3	0.7 ± 0.04	0.7 ± 0.02	-1.6 ± 0.7	0.4 ± 0.1	0.3 ± 0.1
		Hummock	17.3 ± 3.5	0.7 ± 0.02	0.8 ± 0.02	-0.9 ± 0.7	0.4 ± 0.01	0.2 ± 0.0
	Poor Fen	Hollow	55.6 ± 3.4	0.8 ± 0.2	0.9 ± 0.00	-0.5 ± 0.7	0.5 ± 0.03	0.6 ± 0.1

		Hummock	47.3 ± 2.0	0.3 ± 0.2	0.8 ± 0.01	-0.4 ± 0.5	0.5 ± 0.02	0.3 ± 0.01
	Rich Fen	Hollow	46.7 ± 2.5	0.3 ± 0.01	0.9 ± 0.01	0.2 ± 0.2	0.4 ± 0.03	0.6 ± 0.01
		Hummock	41.7 ± 4.4	0.6 ± 0.1	0.9 ± 0.02	0.3 ± 0.2	0.4 ± 0.1	0.5 ± 0.1
Sph mag	Initial (mg g^{-1})	--	--	45.8 ± 1.8	43.5 ± 8.0	359.8 ± 144.4	619.5 ± 13.2	4.1 ± 0.3
	Bog	Hollow	53.3 ± 3.3	0.6 ± 0.01	0.7 ± 0.01	0.7 ± 0.02	0.6 ± 0.1	0.1 ± 0.03
		Hummock	18.3 ± 7.5	0.6 ± 0.01	0.7 ± 0.0	-0.5 ± 0.3	0.2 ± 0.04	0.3 ± 0.02
	Permafrost	Hollow	55.7 ± 2.1	0.9 ± 0.02	0.6 ± 0.01	-0.4 ± 0.1	0.5 ± 0.02	0.3 ± 0.03
		Hummock	25.8 ± 5.9	0.6 ± 0.02	0.7 ± 0.02	0.6 ± 0.3	0.4 ± 0.1	0.2 ± 0.1
	Poor Fen	Hollow	51.1 ± 1.4	0.6 ± 0.01	0.8 ± 0.03	-0.2 ± 0.3	0.4 ± 0.1	0.5 ± 0.1
		Hummock	51.4 ± 1.6	0.5 ± 0.1	0.7 ± 0.03	0.5 ± 0.2	0.5 ± 0.01	0.3 ± 0.04
	Rich Fen	Hollow	51.8 ± 1.4	0.4 ± 0.1	0.9 ± 0.01	0.1 ± 0.2	0.5 ± 0.01	0.7 ± 0.02
		Hummock	47.0 ± 1.2	0.5 ± 0.1	0.9 ± 0.02	0.1 ± 0.3	0.5 ± 0.03	0.6 ± 0.1
Sph rip	Initial (mg g^{-1})	--	--	41.7 ± 1.9	32.4 ± 19.5	135.4 ± 13.6	551.7 ± 25.7	3.9 ± 0.5
	Bog	Hollow	47.1 ± 1.8	0.5 ± 0.1	0.9 ± 0.02	-0.1 ± 0.5	0.4 ± 0.04	0.3 ± 0.02
		Hummock	13.2 ± 2.8	0.9 ± 0.1	0.9 ± 0.02	-1.2 ± 1.3	0.1 ± 0.1	0.3 ± 0.03
	Permafrost	Hollow	54.5 ± 5.3	0.8 ± 0.1	0.9 ± 0.03	-0.9 ± 0.9	0.4 ± 0.02	0.5 ± 0.1
		Hummock	19.7 ± 1.1	-1.1 ± 1.8	0.9 ± 0.03	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.01
	Poor Fen	Hollow	47.5 ± 1.5	0.6 ± 0.1	0.9 ± 0.00	-1.2 ± 0.5	0.3 ± 0.03	0.5 ± 0.00
		Hummock	45.5 ± 2.8	0.8 ± 0.2	0.9 ± 0.01	0.3 ± 0.2	0.3 ± 0.01	0.4 ± 0.03
	Rich Fen	Hollow	40.0 ± 0.8	0.6 ± 0.2	1.0 ± 0.02	0.3 ± 0.1	0.3 ± 0.01	0.7 ± 0.04
		Hummock	39.7 ± 1.6	0.8 ± 0.1	1.0 ± 0.00	0.5 ± 0.04	0.4 ± 0.03	0.7 ± 0.03
Sco sco	Initial (mg g^{-1})	--	--	73.6 ± 1.0	34.1 ± 1.2	383.9 ± 14.2	421.5 ± 0.2	1.1 ± 0.01
	Bog	Hollow	41.8 ± 3.03	0.9 ± 0.1	0.8 ± 0.1	0.2 ± 0.2	0.5 ± 0.1	-0.01 ± 0.1
		Hummock	7.7 ± 0.7	0.8 ± 0.1	0.8 ± 0.01	-0.7 ± 0.3	0.3 ± 0.1	0.3 ± 0.2
	Permafrost	Hollow	40.1 ± 0.6	1.0 ± 0.04	0.5 ± 0.20	-0.5 ± 0.8	0.6 ± 0.1	0.1 ± 0.2
		Hummock	7.7 ± 0.5	0.6 ± 0.1	0.8 ± 0.03	0.2 ± 0.1	0.4 ± 0.2	-0.1 ± 0.1
	Poor Fen	Hollow	42.8 ± 2.2	0.7 ± 0.01	0.8 ± 0.1	-0.03 ± 0.04	0.6 ± 0.04	-0.3 ± 0.7
		Hummock	28.4 ± 6.7	0.5 ± 0.01	0.9 ± 0.03	0.2 ± 0.04	0.6 ± 0.01	-0.05 ± 0.2
	Rich Fen	Hollow	34.9 ± 2.3	0.6 ± 0.00	0.8 ± 0.02	0.02 ± 0.2	0.6 ± 0.00	0.1 ± 0.03
		Hummock	32.3 ± 0.0	0.6 ± 0.03	0.8 ± 0.01	-0.04 ± 0.2	0.6 ± 0.01	0.01 ± 0.04
Tom nit	Initial (mg g^{-1})	--	--	62.5 ± 1.9	32.4 ± 0.3	308.6 ± 2.6	543.5 ± 1.5	1.02 ± 0.05
	Bog	Hollow	41.6 ± 3.3	0.6 ± 0.1	0.9 ± 0.04	-0.04 ± 0.2	0.5 ± 0.1	-0.2 ± 0.2
		Hummock	9.6 ± 4.7	0.7 ± 0.01	0.9 ± 0.02	-2.4 ± 0.6	0.2 ± 0.02	0.1 ± 0.2

	Permafrost	Hollow	40.8 ± 3.2	0.9 ± 0.02	0.2 ± 0.3	-2.0 ± 0.5	0.5 ± 0.1	-0.1 ± 0.4
		Hummock	14.6 ± 1.5	0.5 ± 0.01	0.9 ± 0.04	0.4 ± 0.1	0.6 ± 0.1	0.3 ± 0.2
	Poor Fen	Hollow	42.9 ± 1.4	0.9 ± 0.1	0.6 ± 0.1	0.1 ± 0.2	0.6 ± 0.04	0.1 ± 0.2
		Hummock	34.9 ± 2.2	0.4 ± 0.04	0.9 ± 0.04	0.1 ± 0.1	0.5 ± 0.01	0.2 ± 0.1
	Rich Fen	Hollow	39.9 ± 2.3	0.5 ± 0.1	0.8 ± 0.01	0.3 ± 0.1	0.6 ± 0.04	0.2 ± 0.1
		Hummock	29.7 ± 2.0	0.4 ± 0.01	0.9 ± 0.02	-0.1 ± 0.2	0.5 ± 0.01	0.3 ± 0.02
Ple sch	Initial (mg g^{-1})	--	--	57.9 ± 0.5	56.8 ± 4.0	542.6 ± 201.8	418.5 ± 4.7	3.3 ± 0.6
	Bog	Hollow	35.8 ± 7.9	0.9 ± 0.1	0.7 ± 0.1	0.5 ± 0.2	0.5 ± 0.1	0.2 ± 0.1
		Hummock	6.0 ± 0.6	0.9 ± 0.1	0.8 ± 0.02	0.02 ± 0.1	0.2 ± 0.1	0.4 ± 0.03
	Permafrost	Hollow	39.2 ± 3.8	0.9 ± 0.1	0.5 ± 0.1	0.1 ± 0.2	0.4 ± 0.1	0.4 ± 0.1
		Hummock	12.9 ± 1.9	0.6 ± 0.1	0.8 ± 0.01	0.5 ± 0.1	0.4 ± 0.01	0.3 ± 0.1
	Poor Fen	Hollow	39.4 ± 2.4	0.9 ± 0.1	0.8 ± 0.03	0.3 ± 0.1	0.5 ± 0.03	0.5 ± 0.1
		Hummock	30.4 ± 4.3	0.5 ± 0.03	0.8 ± 0.02	0.5 ± 0.1	0.5 ± 0.03	0.4 ± 0.04
	Rich Fen	Hollow	37.2 ± 3.8	0.8 ± 0.01	0.9 ± 0.03	0.1 ± 0.1	0.4 ± 0.02	0.6 ± 0.02
		Hummock	20.5 ± 5.7	0.6 ± 0.1	0.9 ± 0.02	0.3 ± 0.2	0.4 ± 0.03	0.6 ± 0.03

Table 4-2. Results of two-way analyses of variance assessing the effects of species (8 bryophyte species) and topography (hummock vs. hollow) on decomposition rates for 4 peatland types: A) rich fen, B) poor fen, C) bog, and D) frost mound.

Source	df	Sum of Squares	F	*p*
A) RICH FEN				
Model	15	7232.83	16.54	<0.0001
Species	7	6030.85	29.55	<0.0001
Topography	1	702.17	24.08	<0.0001
Species*Topography	7	377.78	1.85	0.1138
Error	30	874.66		
B) POOR FEN				
Model	15	7852.58	20.40	0.0001
Species	7	6616.74	36.84	<0.0001
Topography	1	152.71	5.95	0.0206
Species*Topography	7	993.00	5.53	0.0003
Error	31	795.42		
C) BOG				
Model	15	8044.83	27.56	<0.0001
Species	7	7388.38	54.25	<0.0001
Topography	1	170.27	8.75	0.0059
Species*Topography	7	357.03	2.62	0.0300
Error	31	603.17		
D) FROST MOUND				
Model	15	7257.00	17.07	<0.0001
Species	7	4549.26	22.92	<0.0001
Topography	1	153.57	5.42	0.0269
Species*Topography	7	2286.99	11.52	<0.0001
Error	30	850.50		

Table 4-3. Results of a stepwise multiple regression assessing the influence of water content and organic fractions on rates of bryophyte decomposition (mg of organic matter lost per g of initial organic matter over a 1-yr field incubation). Organic fractions were measured on fresh moss litter.

Litter quality variables	Partial R^2	Slope ± s.e.	F	*P*
Water-soluble carbohydrates	0.7001	0.12 ± 0.01	396.84	0.0001
Water content	0.0377	-0.06 ± 0.02	24.31	0.0001
Acid-soluble carbohydrates	0.0186	0.63 ± 0.18	12.82	0.0004
Soluble phenolics	0.0153	0.62 ± 0.15	12.26	0.0006

Figure 4-1. Ash-free organic matter losses (mg OM lost g^{-1} initial organic matter mass yr^{-1}) ± s.e. and k (yr^{-1}); same letter superscripts denote nonsignificant mean comparisons. A) Rich fen: mass losses varied by species and by topography, with no significant interaction among effects (Table 4-1). Rich fen hummocks (16.6 ± 1.6^{A}) had higher mass losses than hollows (13.8 ± 1.7^{B}, n=24). In the B) poor fen, C) bog, and D) permafrost mound, organic matter losses varied by a species × topography interaction (Table 1, n=3).

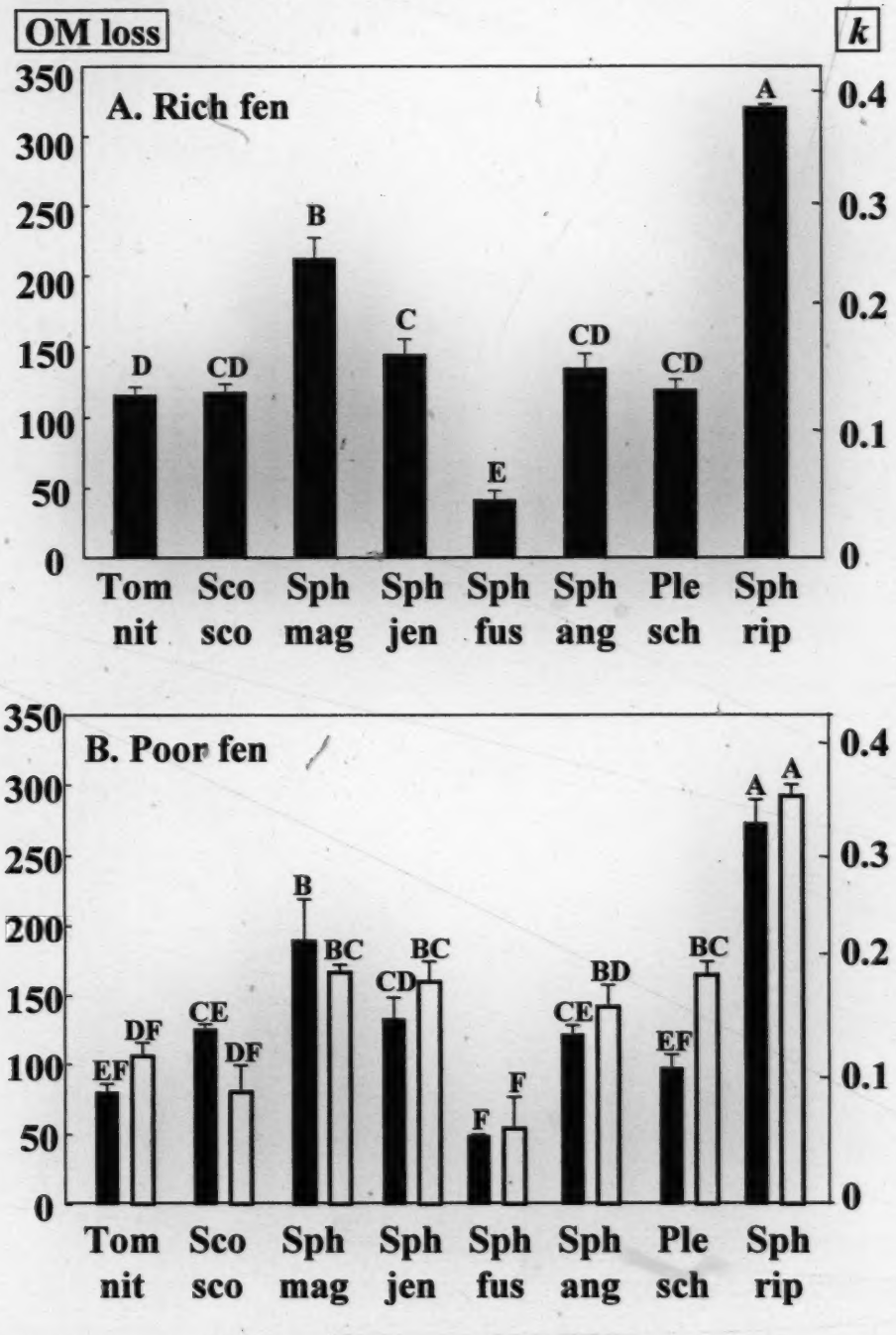


Figure 4-1. continued

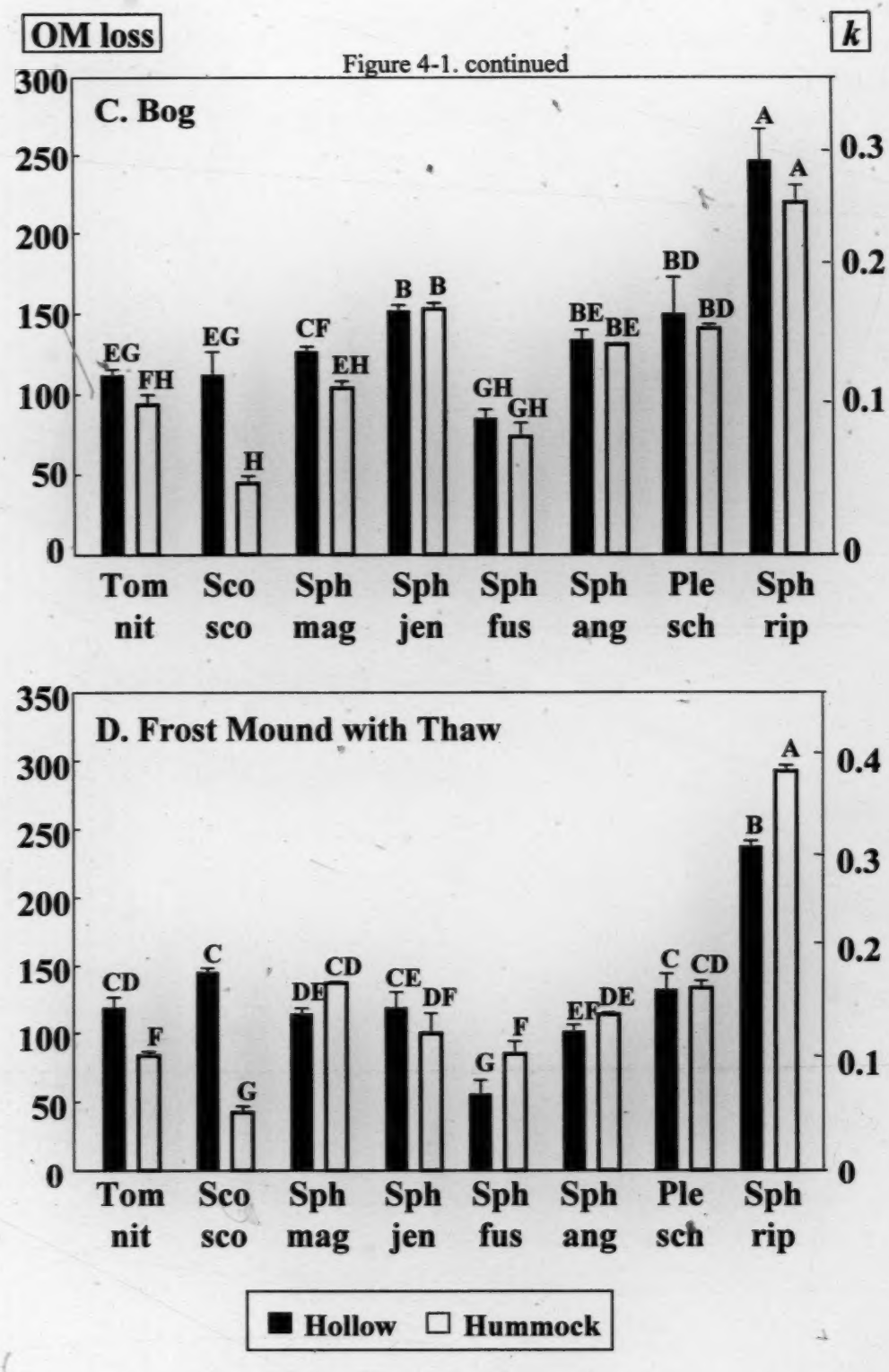


Figure 4-2. Results of a canonical discriminant analysis analyzing organic matter quality variables for eight moss species, including *Sphagnum riparium* (Sph rip), *Sphagnum jensenii* (Sph jen), *Sphagnum angustifolium* (Sph ang), *Sphagnum magellanicum* (Sph mag), *Sphagnum fuscum* (Sph fus), *Pleurozium schreberi* (Ple sch), *Tomenthypnum nitens* (Tom nit), and *Scorpidium scorpiodes* (Sco sco). Three replicate fresh moss samples were quantified for each species. Significant ($p<0.05$) positive or negative Pearson correlations between axes and the organic quality variables are indicated next to each axes. Canonical axis one explained 78 % of the variation in biochemistry data, while axis two explained an additional 16 %.

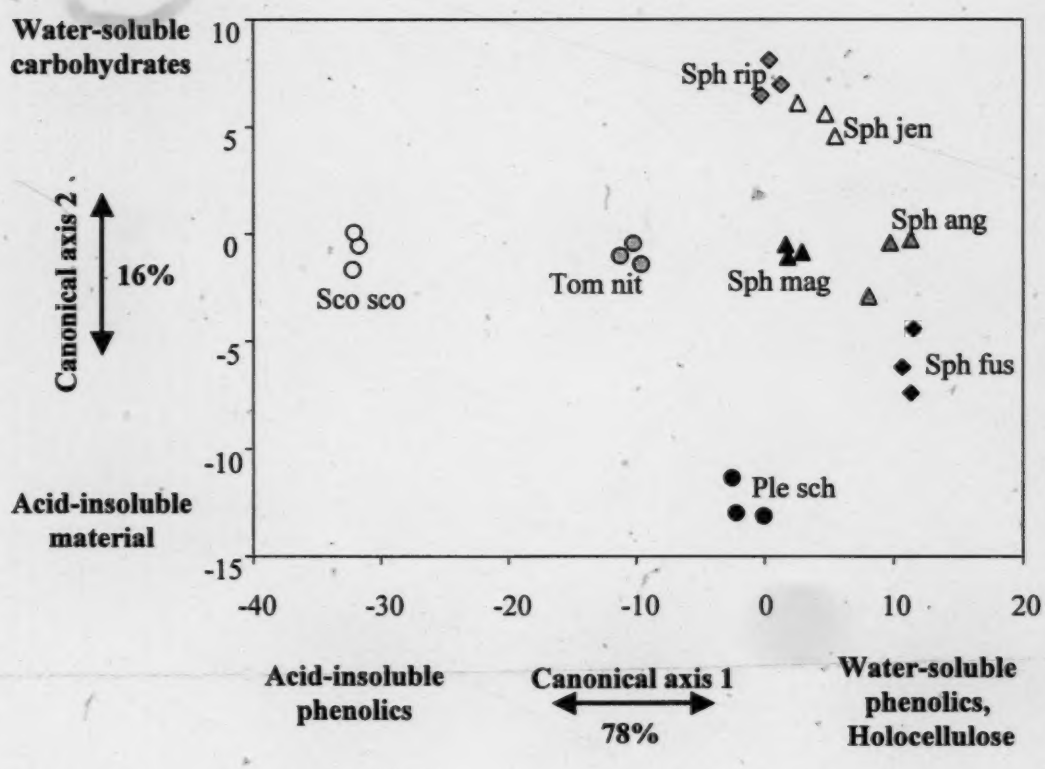
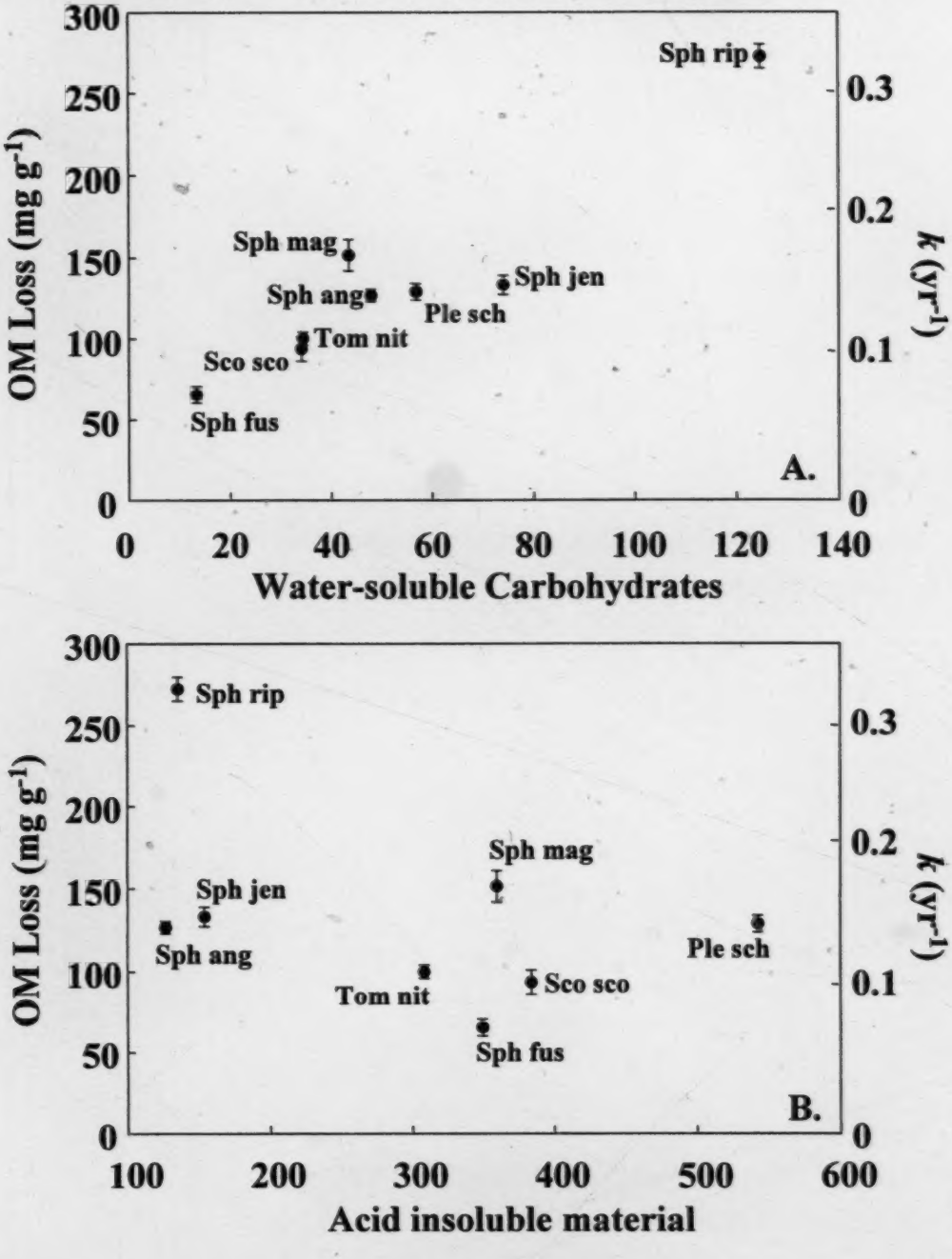


Figure 4-3. Mean organic matter loss (mg of initial OM lost g^{-1} initial organic matter mass yr^{-1}; n=24) and k (yr^{-1}) as a function of **A)** water-soluble carbohydrates (mg g^{-1} ash-free dry mass) and **B)** acid-insoluble material (mg g^{-1} ash-free dry mass) for 8 bryophyte species. Species names abbreviated as in Figure 5-3. Carbohydrate and acid- insoluble material concentrations were quantified on moss subsamples prior to the *in situ* incubations. Soluble carbohydrates explained 70 % of the variation in peat trap decomposition, while acid-insolubles were not significant predictors in a stepwise multiple regression (Table 5-2).



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Chapter 5. Current disturbance and the diminishing peatland carbon sink

Introduction

The Intergovernmental Panel on Climate Change maintains that global carbon (C) sinks and reservoirs must be enhanced and maintained (Watson *et al.* 2000). Disturbances such as fire and insect outbreaks cause declining ecosystem C storage in boreal uplands (Kurz and Apps 1999), but have not been evaluated adequately for peat-accumulating lowlands, despite the importance of peatlands to soil C storage (Gorham 1991; Moore *et al.* 1998). In fact, peatland C budgets typically are constructed for small areas of pristine wetland without consideration for past and ongoing disturbances such as fire, flooding, permafrost melt, and peat extraction. Spatial information on wetland area and land-use is needed, particularly over regional or national scales, to understand current C storage in northern and tropical wetlands (Watson *et al.*, 2000).

Here, I use detailed inventories of peat C stocks across the western Canadian provinces of Alberta, Saskatchewan, and Manitoba produced by extensive mapping and field surveys of peatlands (Vitt *et al.* 2000a). Peatlands in this region cover 365,160 ± 14,606 km^2, or 21% of the landbase, and store 48 ± 5 Pg (=10^{15} g) of C as peat (42 Pg) and living biomass (6 Pg) (Vitt *et al.* 2000a). This C stock represents about 2.1 % of the world's terrestrial C stored on 0.3 % of the world's land surface. These detailed peatland inventories allowed me to estimate the areal extent of ongoing disturbances affecting boreal peatlands of western Canada and to calculate potential impacts on peatland C balance. When possible, I estimate and propagate uncertainties surrounding disturbance parameters, assuming Gaussian distributions.

Carbon Losses from Historical Fires

Long-term peat accumulation rates based on radiocarbon dating average 19.4 ± 2.1 g C m^{-2} yr^{-1}, or 7080 ± 779 Gg (=10^9 g) C yr^{-1} across the entire region (Vitt *et al.* 2000a). As charcoal layers have been identified in peat deposits (Zoltai *et al.* 1998), I note that C losses due to historical fire activity are incorporated into this long-term accumulation rate. Radiocarbon-based accumulation rates, therefore, underestimate long-term net peatland C accumulation.

In continental boreal regions, dry, wooded peatlands burn more readily than wet open or shrub-dominated peatlands. Charcoal frequencies in long-term peat stratigraphies suggest that 0.25 % of continental peatlands in North America have burned annually (Zoltai *et al.* 1998). I multiplied 0.25 % by the total aerial extent of wooded peatlands in the study area (235,460 ± 9,418 km^2) (Vitt *et al.* 2000a) to calculate that 580 ± 23 km^2 of wooded peatland area burned historically each year. Published estimates of C losses due to peatland fires average 3.2 ± 0.4 kg C m^{-2} per fire event (n=6 studies; ranging from 2.1 to 4.9 kg C m^{-2} with a median value of 2.7 kg C m^{-2}) (Turetsky and Wieder 2001). The historical burned area (580 ± 23 km^2) was multiplied by 3.2 ± 0.4 kg C m^{-2} to calculate a regional historical combustion rate of 1860 ± 242 Gg C yr^{-1}. I added 1860 ± 242 Gg C yr^{-1} to the long-term regional accumulation rate based on radiocarbon dating (7080 ± 779 Gg C yr^{-1}) to calculate C accumulation under no disturbance (Table 5-1). Long-term C accumulation in the absence of fire is estimated at 8940 ± 816 Gg C yr^{-1} (Table 5-1), 26 % higher than previous estimates. Thus, following the practice of using long-trends to estimate current C accumulation rates, peatlands across continental,

western Canada today are accumulating 24.5 ±2.4 g C m^{-2} yr^{-1}.

Carbon Losses from Current Fires

The Large Fire Database (Stocks *et al.* in review) compiles provincial data recording fires over 200 ha in size, which represent more than 95 % of the total area burned in western Canada. I overlaid mean proportions of land burned in 1 ° latitude × 1 ° longitude grids from 1980 to 1995 (Stocks *et al.*, in review) on digitized peatland distributions (Vitt *et al.* 2000a) to calculate a current burned area of peatlands across the study region of 1470 ± 59 km^2 yr^{-1}. While it seems likely that fires in the study area will impact upland forest to a greater extent than peatlands, the relative susceptibility of peatlands to burning is unknown. I assumed that open peatlands, representing about 40 % of the total peatland area in the region, do not burn and excluded them from my analysis. I multiplied 1470 ± 59 km^2 by average combustion rates (3.2 ± 0.4 kg C m^{-2}) (Turetsky and Wieder 2001), to calculate a regional combustion rate of 4704 ± 618 Gg C yr^{-1} (Table 5-1).

Because peatland fires remove vegetation, peatlands function as net sources of atmospheric C post-fire, and continue to do so until vegetation recovers to the pre-fire level of net primary production. The strength of the regional post-fire C source depends on the area of peatland burned annually, the magnitude of immediate C losses after fire, the time to recovery to pre-fire net primary production levels, and the shape of the recovery trajectory (Figure 5-1). I know of no data on post-fire C fluxes from burned peatlands. However, based on an empirical modeling approach, decomposition in the upper 30 cm of peat, where most organic matter mineralization probably occurs, was estimated at 183-243 g organic matter m^{-2} yr^{-1} (mean of 209 g m^{-2} yr^{-1}) for three sites in

Alberta (assuming that peat is 47 % C, equivalent to 100 g m^{-2} yr^{-1} of CO_2-C loss) (Wieder 2001). Using this value for initial post-fire mineralization, and peatland recovery times and trajectories outlined in Figure 5-1, I estimate a regional enhanced post-fire peatland mineralization rate of 1578 ± 696 Gg C yr^{-1}. The combined direct and indirect effects of peatland fire amounts to a source of C to the atmosphere of 6282 ± 931 Gg C yr^{-1} (Table 5-1).

Permafrost Melt

Approximately 2630 ± 105 km^2 of permafrost in peatlands has melted over the past ~100 yr in western Canada; permafrost degradation continues today (Vitt *et al.* 1994). Assuming constant degradation rates (2630 ± 105 km^2 ÷ 100 y), I estimate that 26.3 ± 1.1 km^2 of permafrost in peatlands melts annually. Permafrost melt in peatlands converts permafrost mounds to wet depressions called internal lawns. Net C accumulation is greater in internal lawns than in permafrost mounds by 44 ± 25 g C m^{-2} yr^{-1} (Chapter 2), for at least a century after initial melt (Turetsky *et al.* 2000; Chapter 2). Therefore, I multiplied 2630 ± 105 km^2 of regional melt by 44 ± 25 g C m^{-2} yr^{-1} to estimate a regional enhanced C sink associated with the conversion of permafrost mounds to internal lawns of 116 ± 37 Gg C yr^{-1} (Table 5-1).

Peat Extraction

In 1997, 78 Gg C (assuming peat is 47 % C) was harvested as peat from three peat mines in Saskatchewan and Manitoba, and two mines in Nova Scotia (Statistics Canada 1997). These provincial data are not reported separately, therefore, I assumed 83% of

this harvest (65 Gg) occurred in western Canada (Statistics Canada 1997; G. Hood, Canadian *Sphagnum* Peat Moss Association, personal communication, 2001). 70 Gg C also was harvested in Alberta (Statistics Canada 1997) for a total regional export of 135 Gg C across western continental Canada. Approximately 23 % of the 160 km^2 of peatland harvested across Canada is located in the prairie provinces (37 km^2). After harvest of the upper peat layers, an abandoned peat mine is a source of atmospheric C, as ongoing decomposition in the residual peat exceeds the negligible net primary production at the denuded peat surface. I multiplied mineralization rates from harvested peatlands in eastern Canada and Europe (470 ± 108 g C m^{-2} yr^{-1}) (Waddington and Price 2000; Sundh *et al.* 2000) by 37 km^2 to estimate a regional enhanced mineralization rate of 17.4 ± 4.0 Gg C yr^{-1} (Table 5-1). Peat mines have average lifetimes of 32.5 yr (Keyes 1993), suggesting that 1.1 km^2 of pristine peatland is developed annually.

Hydroelectric Reservoirs

Manitoba has used hydroelectric generation as an energy source for nearly 80 years. Peatland inventories (Vitt *et al.* 2000a) near Manitoba's hydroelectric generating stations suggest that 780 ± 3 km^2 of peatland has been flooded, corresponding to an average of 9.6 ± 0.04 km^2 of annual flooding over 80 years. Carbon emissions from peatland reservoirs in western Ontario and Finland, ranging from 2 to 28 years in age post-flooding, average 102 ± 24 g C m^{-2} yr^{-1} (Kelly 1997; Hellsten *et al.*, 1996). I multiplied 780 km^2 by mean reservoir C emissions rates (102 ± 24 g C m^{-2} yr^{-1}) to estimate a regional enhanced mineralization rate associated with peatland conversion to reservoirs of 80 ± 19 Gg C yr^{-1} (Table 5-1).

Oil Sand Mining

I estimate that 22% of current oil sands surface leases (Oil sands mining land use committee 1998) is covered by peatlands (15.5 ± 0.6 km^2) containing 2400 ± 168 Gg C (Vitt *et al.* 2000a). To my knowledge, current oil sands mining practice includes removal of peat overburden and stockpiling for potential reclamation use. Peat used in soil organic matter amendments eventually will decompose under aerobic conditions. I assumed a complete loss of extracted C over a 50 yr time interval to estimate a disturbance-related flux of 48 ± 3 Gg C yr^{-1} (Table 5-1).

Peatland conversion to agriculture or forestry

In some peat-rich regions, ongoing development results in the conversion of native peatlands to either agriculture or forestry land uses, both of which are likely to alter C balances. In western Canada, however, there is no present conversion of native peatland to cropland (Dumanski *et al.* 1998). There also is little interest today in draining or fertilizing peatlands for managed forestry uses, particularly in Saskatchewan and Manitoba (Haavisto and Jeglum 1991).

Discussion

Globally, peatlands represent a large C stock, estimated at 397-455 Pg C (Gorham 1991; Zoltai and Martikainen 1996) or one-third of the world's soil C pool. Carbon sink/source relationships in peatlands can be estimated through measurements of both net primary production and decomposition rates in peatlands, with subsequent estimation of

C storage capacity (Thormann *et al.* 1999). However, this approach largely is confounded by methodological limitations, as well as by large spatial and temporal process variability. Net ecosystem C fluxes have been obtained via eddy covariance or chamber techniques in subarctic and boreal peatlands (cf. Friborg *et al.* 1997; Lafleur *et al.* 1997; Suyker *et al.* 1997; Goulden *et al.* 1998; Waddington and Roulet 2000). Yet these studies mainly have been conducted in eastern- or mid- North America where different moisture regimes and underlying substrates make application to western continental Canada imprudent. Constructing regional C budgets from net ecosystem flux requires temporally and spatially intensive measurements coupled to models for larger-scale extrapolation. Alternatively, my approach capitalizes on the long-term records stored in vertically accumulating peat across western boreal Canada. I use current peat volumes on the landscape, obtained from detailed aerial photograph inventories and peat depth information from 818 sites, corrected for long-term catotelm decay (Vitt *et al.* 2000a). While C accumulation in the region has decreased since the mid-Holocene, I estimate current accumulation rates (accounting for historical fires) at 24.5 g m^{-2} yr^{-1}. This value is only slightly lower than model-derived estimates for current net C accumulation in the upper 30 cm of peat of 34-52 g C m^{-2} yr^{-1} for three sites in Alberta (Wieder 2001), which do not include C losses from decomposition deeper in the peat profile.

Climatic fluctuations clearly have influenced trends in peatland C storage across western Canada (Vitt *et al.* 2000a), yet to date the various natural and anthropogenic disturbances affecting peatland C stocks have not been evaluated. I estimate that about 47,600 km^2 of peatland are affected by recent disturbance, or 13 % of the regional

peatland area (Table 5-1). New disturbances cumulatively affect about 1500 km^2, or 0.4 %, of peatlands each year across western Canada (Table 5-1). Therefore, assuming an even distribution of disturbances over the landscape, a typical boreal peatland may experience disturbance in some form about every 250 years.

Clearly, however, disturbance across the boreal forest is not spatially homogeneous, particularly in peatlands where permafrost patterning is important. The degradation of 2630 km^2 of permafrost in peatlands is a relatively recent phenomenon in the boreal forest, likely due to climatic warming over the past 100-150 years (Vitt *et al.* 1994). Ongoing permafrost melt accounts for only about 2 % of new areal peatland disturbance (26.3 $km^2\ yr^{-1}$; Table 5-1). However, permafrost thaw has long-term effects on peatland water tables and albedos, and results in distinct species composition compared to surrounding peatlands for at least a century (Vitt *et al.* 2000b).

Lightning-initiated fires also are common in western Canada, representing 98 % of the annual areal peatland disturbance (Table 5-1). Fires in the western boreal forest have increased since the 1980s (Kurz and Apps 1999), but an increase in peatland fires in recent years previously has not been documented. Across the study region, I estimate that as much as 1470 km^2 of peatland burns currently each year, an area 2.5-fold greater than the historical estimate. This change in burn areas may be attributed to methodological differences and/or increasing fire regimes in recent years.

Permafrost melt and fire have very different impacts on the storage of soil C. Melting permafrost increases peatland C accumulation in the study area (Turetsky *et al.* 2000; Chapter 2) by stimulating bryophyte primary production. The strength of this sink will be enhanced if rates of permafrost degradation increase under a warming climate.

Fire, however, results in the immediate release of CO_2, CO and CH_4 to the atmosphere through combustion and increased post-fire decomposition rates through increased temperatures and increased nutrient supply from ash (Hogg *et al.* 1992; Wardle *et al.* 1998). My estimates suggest that the immediate impact of combustion releases about 4700 Gg of C to the atmosphere, about 3 times greater than emissions due to enhanced post-fire mineralization. Fire clearly is the most important disturbance affecting peatland C emissions, accounting for 97 % of total disturbance-related C losses (Table 5-1).

Certain human activities remove large amounts of organic matter from peatlands that either are exported (e.g. peat extraction for horticultural products) or stockpiled (e.g. oil sand development), and subsequently oxidized under aerobic conditions. Hydroelectric reservoirs are large sources of greenhouse gases to the atmosphere, particularly those reservoirs inundating peatlands (St. Louis *et al.* 2000; Kelly 1997). I estimate that these anthropogenic disturbances contribute to 280 Gg of C losses through a combination of C removal from the landscape and changing mineralization rates on site (Table 5-1).

In total, C emissions from disturbed peatlands across western Canada totaled 6446 ± 932 Gg C yr^{-1} and reduced regional C accumulation by 85 % compared to the no-disturbance scenario (Table 5-1). Combustion during fire clearly leads to large C losses to the atmosphere, but also is associated with relatively large error estimates due mostly to error in combustion rates rather than current burn areas (Table 5-1). Additional studies focusing on combustion during peatland fires will help to determine whether uncertainties in our approach are attributed to measurement error or variability in fire intensity. Carbon fluxes associated with enhanced mineralization in burned peatlands

also are large (Table 5-1), indicating a strong need for field measurements of post-fire C fluxes in peatlands. This approach suggests that fire monitoring programs in the boreal forest should follow both fire frequencies and burn intensities to best assess total C loss from organic soils.

Conclusion

I show that natural and anthropogenic disturbances have a substantial influence on soil C storage in the boreal forest that only can be recognized at regional scales of study. This approach relies upon all available information on peatland C stocks and current levels of disturbance and development across western Canada, and points to the need for more mechanistic understanding of lowland disturbances and peatland recovery. My assessment of regional C stocks suggests that peatlands accumulate 24.5 g C m^{-2} yr^{-1} during periods of no disturbance (Table 5-1). However, these average C accumulation rates are reduced to 3.7 g C m^{-2} yr^{-1} under contemporary levels of disturbance and development across the study region in western boreal Canada.

Consideration of changing disturbance regimes with near-future climate change also must be evaluated across broad scales. Fire is more important to organic soil C stocks than direct human activities such as flooding, peat extraction, and oil sands development. Global circulation models predict temperature increases of 1-5 °C in boreal and subarctic regions with a doubling of atmospheric CO_2 (Moore *et al.* 1998). Both fire and permafrost melt largely are controlled by climate, and may become more important to peatland C balances in the future under these climate change scenarios (Vitt *et al.* 2000b; Stocks 1998). Permafrost melt in peatlands is not independent of fire in boreal landscapes, and will serve as a small buffer against future C losses. However,

predicted increases in fire frequency and intensity under a warmer, drier climate in western boreal forest (Stocks 1998) will have large consequences for peatland C storage.

I argue that a true understanding of C sinks at northern latitudes must account for disturbances in both upland and lowland systems. A similar ecosystem approach may reconcile C emission estimates from recent boreal forest models differing in organic soil and disturbance representation (cf. Amiro *et al.* 2001; Kasischke *et al.* in review). According to our estimates, increases in both the area of peatland burned annually (km^2 yr^{-1}) and the intensity of organic matter combustion (g C m^{-2} $fire^{-1}$) of 17% would convert these northern peatlands to a net C source to the atmosphere.

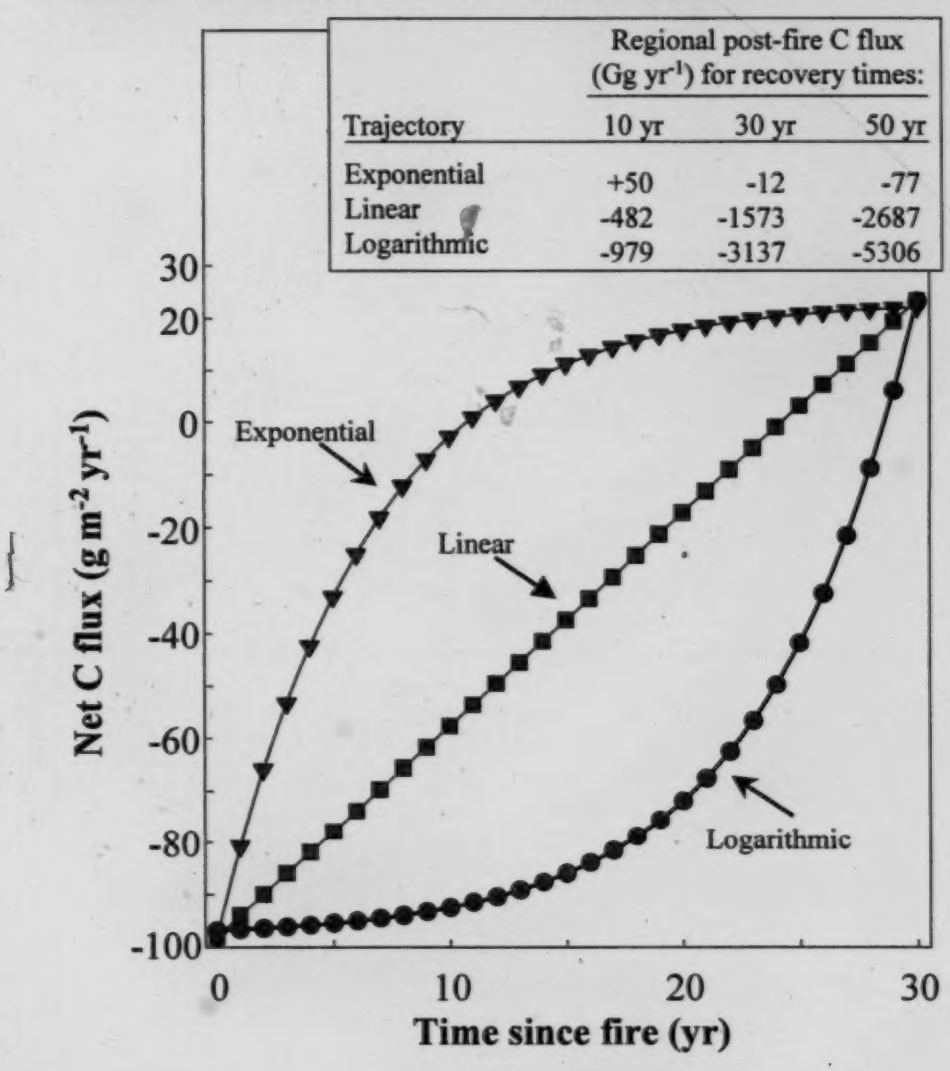
Table 5-1. Peatland carbon fluxes across western Canada under current disturbance regimes.

Disturbance	Total Extent km^2	Annual Disturbance $km^2\ yr^{-1}$	Mechanism of C Flux	C flux $g\ C\ m^{-2}\ yr^{-1}$	C flux $(Gg\ C\ yr^{-1})^1$
No disturbance	365,160 ± 14,606		Production > decomposition	24.5 ± 2.4[3]	+ 8940 ± 816[2]
Current fire	44,100 ± 1764[4]	1470 ± 59	Combustion	3200 ± 400	- 4704 ± 618
			Mineralization		-1578 ± 696
Permafrost melt	2630 ± 105	26.3 ± 1.1	Enhanced plant production	38 ± 9	+ 116 ± 37
Peat extracting	37[6]	1.1[6]	Direct harvest	3649[6]	- 135
			Mineralization	470 ± 108	- 17 ± 4
Reservoirs	780 ± 3.1	9.6 ± 0.04	Mineralization	102 ± 24	- 80 ± 19
Oil sands mining	16 ± 0.6	0.3 ± 0.01	Direct removal	2400 ± 168	- 48 ± 3
Total disturbance	47,563 ± 1767	1507 ± 60	Total disturbance losses	9883 ± 478	-6446 ± 932
Undisturbed area	317,580 ± 14,713		Production > decomposition	24.5 ± 2.4[4]	+ 7781 ± 843[5]
C balance	365,160 ± 14,606		Production > decomposition + disturbance-losses		+ 1335 ± 1257

[1]Positive C fluxes represent net sinks of atmospheric C while negative fluxes represent net sources of atmospheric C.
[2]7080 ± 779 Gg C yr^{-1} (Vitt *et al.* 2000a)) + 1860 ± 242 Gg C yr^{-1} (accounting for C loss through historical fires)
[3]Rates of C accumulation accounting for historical fires: (8940 ± 816 Gg C) ÷(365,160 ± 14,606 km^2)
[4]1470 km^2 × 30 yr average peatland recovery time (Figure 5-1)
[5]total peatland area minus disturbed peatland area, accumulating at 24.5 ± 2.4 g C $m^{-2}\ yr^{-1}$
[6]error estimates not available

Figure 5-1. Recovery of peatland carbon accumulation following fire. Positive and negative C fluxes represent net sinks and sources of atmospheric C, respectively. Diminished NPP and enhanced decay occur post-fire. Although vegetation typically reestablishes within 20 yr (Zoltai *et al.* 1998), no data are available regarding the length of recovery to pre-fire net C accumulation (24.5 ± 2.4 g C m^{-2} yr^{-1}; Table 5-1) or the recovery trajectory. Here, post-fire C fluxes are estimated assuming 100 g C respiration m^{-2} yr^{-1} after fire (cf. Wieder, 2001) and using a cohort model dividing the regional area of peatland currently burned annually (1470 ± 59 km^2) into 9 categories following one of three recovery trajectories and one of three recovery times. Post-fire trajectories of peatland recovery are plotted for a 30 yr recovery, while the inset shows C fluxes for each cohort. Long recovery times and logarithmic trajectories may be more characteristic of large fires in relatively cool and dry subarctic or high boreal peatlands, while short recovery times and exponential trajectories may be more characteristic of smaller fires in relatively warm and moist low boreal peatlands.

	Regional post-fire C flux (Gg yr^{-1}) for recovery times:		
Trajectory	10 yr	30 yr	50 yr
Exponential	+50	-12	-77
Linear	-482	-1573	-2687
Logarithmic	-979	-3137	-5306



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Chapter 6. Peat and permafrost summary

Boreal carbon stocks

Northern soils in boreal and subarctic regions represent a major terrestrial C reservoir that slowly has accumulated since the last deglaciation (Harden *et al.* 1992) (Figure 6-1). While terrestrial systems in boreal regions cover less than 20% of the earth's land surface, they store more than 30% of all terrestrial carbon mainly in soils. Today, about 500 Pg C is contained in northern soils as a result of low rates of decomposition, under cool moist climatic conditions, rather than high rates of primary productivity (Figure 6-1). Across the prairie provinces of western continental Canada (Alberta, Saskatchewan, and Manitoba), about 85 % of stored soil C lies in deep peat deposits that cover approximately 365,000 km^2 or 21% of the region (Figure 6-2) (Bhatti *et al.* 2002; Vitt *et al.* 2000a). Western boreal peatlands, then, store a disproportionate amount of C on the landscape that has accumulated over the past ~8 000 yr at average rates of 25 g C m^{-2} yr^{-1} (Chapter 5).

While peatlands today are believed to function as net sinks for atmospheric CO_2 and as net sources for CH_4 (Figure 1-1) (Roulet *et al.* 1992; Moore *et al.* 1998; Whalen and Reeburgh 2000), recent C balance studies have demonstrated that individual peat deposits may switch between net C sinks and sources interannually (Alm *et al.* 1997; Rivers *et al.* 1998; Waddington and Roulet 2000). Northern ecosystems at high latitudes are expected to receive the most pronounced warming in response to rising levels of greenhouse gases in the atmosphere (Raisanen 1997). Thus, changing temperature and

precipitation regimes in the future may have strong influence on peatland C storage by influencing photosynthesis, decomposition, succession, and fire regimes.

In general, the majority of peatland C studies have been conducted over small spatial scales in pristine, *Sphagnum*-dominated peatlands. There are few data, for example, comparing C storage or emissions in peatlands across heterogeneous boreal landscapes, despite large variability occurring among northern peatlands in species composition and moisture availability. Near the southern limit of permafrost, the presence or absence of permafrost causes major changes in hydrology, insolation, topography, and species composition in peatlands (Camill 1999; Zoltai 1995; Vitt *et al.* 2000b). Permafrost patterning, then, may have important consequences for C cycling in peatlands (Bubier *et al.* 1995; Liblik *et al.* 1997) and for our understanding of the future responses of boreal systems to climatic change. Because peat has accumulated since the last glacial retreat (over the past ~8,000 years), the study of peat deposits can evaluate biogeochemical responses to environmental variability on scales ranging from years to millennia. Thus, my work combines analyses of current plant- and microbial-driven processes with historical perspectives obtained from organic soil records.

Permafrost dynamics and ecosystem function

Permafrost underlies 1/3 of northern peatlands, and ranges from continuous coverage in the arctic to discontinuous patchy distributions further south in the boreal forest. During the Little Ice Age, permafrost reached its maximum southern-most extent in boreal western Canada with 28,800 km^2 of permafrost present in peatlands (Vitt *et al.* 2000b). Peatlands underlain by permafrost (i.e., frost mounds, palsas, or peat plateaus)

are relatively well-drained, as freezing soil water elevates the peat surface through the volume expansion of freezing soil water. As such, permafrost peatlands in boreal regions are dominated by dry-adapted species such as lichens (*Cladina* spp.) and feather mosses (*Hylocomium splendens*, *Pleurozium schreberi*), and tend to have dense canopies of black spruce (*Picea mariana)* (Vitt *et al.* 2000b).

Surface peat deposits in frost mounds are dominated by dry woody material that has accumulated irregularly over the past ~100 yr (Chapter 2). Microbial activity probably is inhibited within ice lenses, although decomposition can occur above the permafrost table. While frost mounds emitted CO_2 at rates similar to unfrozen bogs, rates of CH_4 emission across the peatland/atmosphere boundary are much lower in frost mounds (Chapter 3). In fact, these systems occasionally consume methane from the atmosphere, suggesting that methane-oxidizing bacteria occupy the dry soil environments of permafrost acrotelms.

Near its southern limit in the boreal forest, permafrost is restricted almost exclusively to peatlands. Degradation of southern permafrost is a relatively recent phenomenon of the past century, and may be related to increasing fire frequency or a recent warming of the southern boreal region (Halsey *et al.* 1995; Zoltai 1995; Vitt *et al.* 2000b). Permafrost collapse causes the soil surface to subside, creating wet poor fens (internal lawns) dominated by *Carex* spp., *S. riparium* and *S. angustifolium* (Vitt *et al.* 1994; Turetsky *et al.* 2000). Internal lawns are characterized by higher rates of peat accumulation compared to neighbouring frozen or unfrozen bogs, therefore, permafrost melt increases terrestrial C storage (Chapter 2). However, internal lawns also are associated with high rates of CH_4 emission (Chapter 3). Because CH_4 is a powerful

greenhouse gas, with 18-20 times greater radiative strength than CO_2 (Schimel *et al.* 1996), the magnitude of CO_2 and CH_4 gas fluxes across discontinuous permafrost will be an important factor in determining boreal carbon budgets. Internal lawns sequester more CO_2, but are stronger sources of CH_4 than frozen or unfrozen bogs. Therefore, melting of permafrost potentially has both positive and negative feedbacks to climate change (Figure 6-3).

Peat accumulates where the production of plant biomass in a given area exceeds rates of microbial decomposition. Increases in both surface peat accumulation (Chapter 2) and net ecosystem respiration (Chapter 3) following permafrost melt suggests that plant primary production also must be stimulated in internal lawns. The thawing of permafrost creates very wet environments interspersed within a relatively dry continental landscape. It seems likely that high rates of bryophyte production is in direct response to increasing moisture availability.

Species controls on ecosystem function

Permafrost thaw in peatlands creates saturated fens dominated by wet-adapted *Sphagnum* and *Carex* spp. Changing hydrology and/or unique species assemblages in areas of thermokarst may control observed changes in ecosystem function, such as increased organic matter storage (Chapter 2) and decomposition (Chapter 3). Investigations into biological and environmental controls on bryophyte decay in peatlands reveal that short-term decomposition varies significantly among peatland bryophyte species (Chapter 4). *Sphagnum riparium*, common to internal lawns, decomposed quickly during *in situ* incubations, losing 26 % of its initial mass across a

variety of peatland types. Alternatively, *S. fuscum*, a common bog hummock species, lost an average of 7 % of initial mass. *S. riparium* tissue corresponds to greater concentrations of water-soluble carbohydrates than other *Sphagnum* species, suggesting that this moss is divesting more of its resources than other mosses into the production of labile C substrates to sustain high growth rates (Pakarinen and Vitt 1974). In turn, this C allocation strategy provides a labile C pool that easily is degraded through microbial attack, thus explaining the high mass loss values for this species.

This study indicates that the life history strategies of moss species may have important feedbacks to peatland ecosystem functions such as decomposition. Future work should investigate the influence of species or plant functional groups on production and decay rates to improve our ability to scale ecosystem processes across large regions. The timing of post-melt succession in internal lawns is poorly understood (but see Beilman 2001), but will be important in western Canada with future climatic warming and permafrost degradation.

Landscape scaling

Once initiated, the thaw of permafrost rapidly changes the ecology, biogeochemistry, and hydrology of peatlands. Permafrost in peatlands has degraded since the Little Ice Age across a broad region of boreal Canada. Remote sensing and peatland mapping show that about 10% of permafrost has melted to form internal lawns (Vitt *et al.* 2000b). Another 22% of permafrost is present in peatlands with mean annual temperatures above 0 °C, suggesting that large areas of permafrost peatlands are in

disequilibrium with the current climate and are extremely sensitive to future climatic flux (Halsey *et al.* 1995; Vitt *et al.* 2000b). Permafrost thaw causes increasing net organic matter accumulation (Chapter 2) due to enhance bryophyte growth. Across continental boreal regions of North America, permafrost melt has increased regional C sinks by an estimated ~160 Gg C yr^{-1} (Chapter 5).

A regional contemporary C budget for peatlands located across western Canada (Chapter 5) shows that permafrost melt is the only ongoing disturbance that represents a negative feedback to future greenhouse gas warming. Fire and anthropogenic land-uses such as peat extraction, oil sand mining and hydroelectric reservoir creation lead to net releases of C to the atmosphere. Fire clearly is the most important disturbance affecting peatland C emissions, accounting for 97 % of total disturbance-related C losses (Table 5-1). During fire, C is immediately released to the atmosphere as CO_2, CO and CH_4 through combustion and is released over time via increased post-fire decomposition rates through increased temperatures and increased nutrient supply from ash (Hogg *et al.* 1992; Wardle *et al.* 1998).

Both fire and permafrost melt largely are controlled by climate, and may become more important to peatland C balances under future climate change scenarios (Vitt *et al.* 2000b; Stocks 1998). Permafrost melt in peatlands is not independent of fire in boreal landscapes, and will serve as a small buffer against future C losses. The presence of permafrost increases both fire frequency and severity in peatlands due to dry soil conditions above the permafrost table and the accumulation of dry fuels in feathermoss/lichen groundlayers and *P. mariana* litter. Increased fire frequencies across the boreal forest due to warmer, drier climatic conditions will cause more widespread

permafrost melt in peatlands. Initially protected from fire losses due to saturation and low fuel availability in recently melted areas, this carbon reserve will become more susceptible to fire losses as peat accumulates above the water table and creates drier soil conditions. Thus, the timing of internal lawn succession or development will be important to 1) patterns of surface organic matter accumulation, and 2) fire regimes in boreal lowlands. Internal lawn development, therefore, has major implications for the accumulation and retention of soil C at northern latitudes.

Conclusions

Permafrost dynamics in peatlands are controlled by complex vegetation, climate, and disturbance factors at both local and regional scales that also interact to influence terrestrial C stocks (Figure 6-3). Permafrost at its southern limit across western Canada is degrading to form wet depressions on the landscape called internal lawns. Internal lawns are colonized quickly by semi-aquatic species such as *S. riparium*. These species thrive on the increased water availability generated during thermokarst, and produce high concentrations of simple carbohydrates to sustain fast growth rates. This C allocation response, in turn, stimulates microbial activity by creating a soluble pool of C substrates that easily are decomposed. Nonetheless, permafrost melt in boreal peatlands stimulates soil C storage, pointing towards the importance of the response in bryophyte production in determining C balance post-melt. Permafrost will continue to degrade across boreal regions under a warming climate. Changing precipitation regimes also are predicted for North America, and decreasing precipitation likely will lead to more frequent and severe fires in boreal landscapes. Fires impacting peatlands in the future will 1) release large

amounts of C to the atmosphere through organic matter combustion, diminished plant production, and enhanced post-fire decomposition, and 2) accelerate permafrost melt leading to a small buffer against future C losses.

Figure 6-1. Schematic of soil carbon stocks (Pg C) and rates of net primary production (NPP in Pg C yr^{-1}) across the globe. Boreal soils represent a major reservoir of stored carbon that have accumulated since the last deglaciation. Relatively low rates of boreal NPP suggest that soil carbon stocks are a result of low rates of decomposition under the cool climates typical of northern latitudes. Data taken from Zoltai and Martikainen (1996) and Schlesinger (1997).

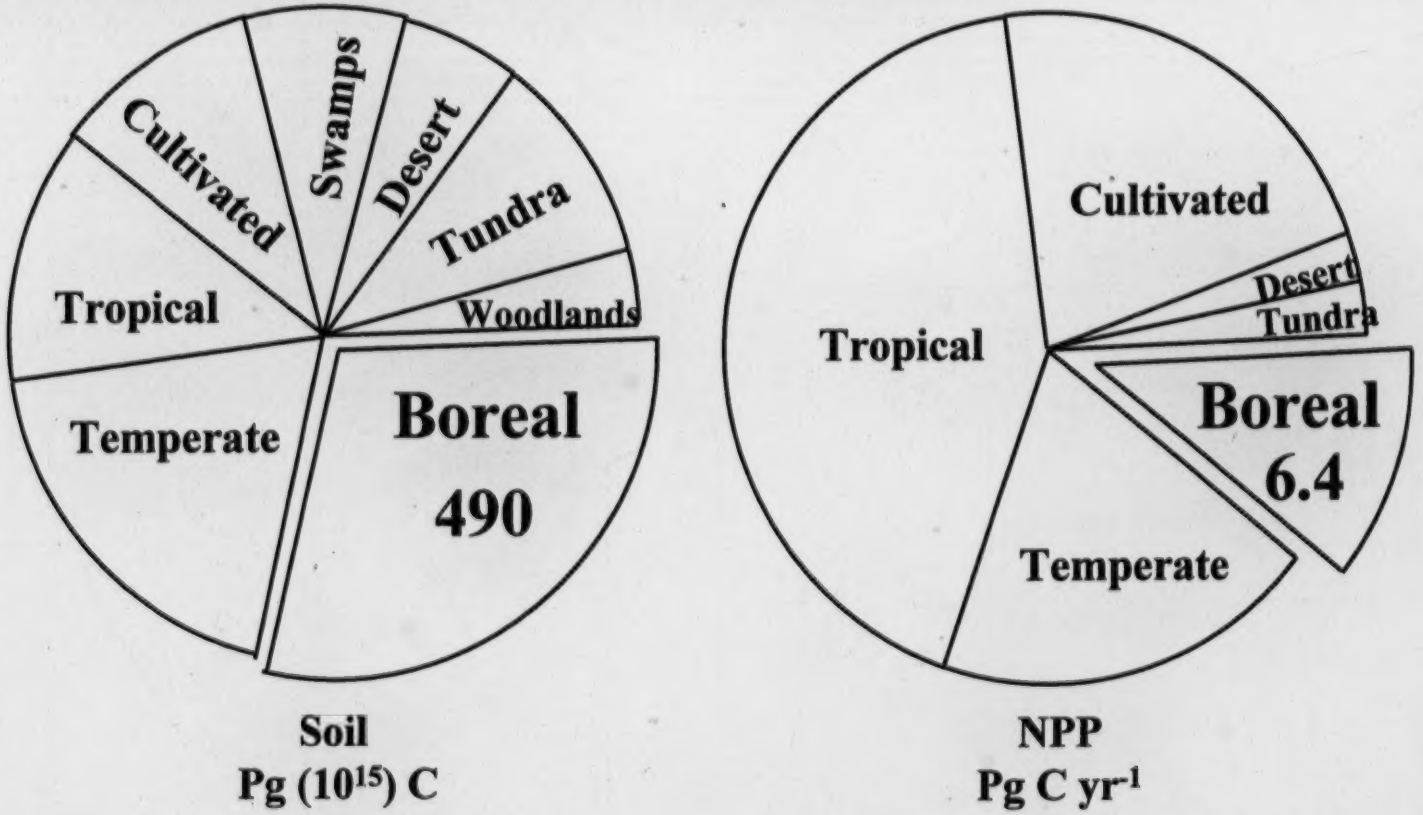


Figure 6-2. Across western boreal Canada, peatlands store about 42 Pg of soil C, compared to only 0.4 Pg soil C stored in boreal uplands. Therefore, peat deposits represent about 85 % of soil C, but cover only about 21% of this region. Data taken from Vitt *et al.* (2000a) and (Bhatti *et al.* 2002).

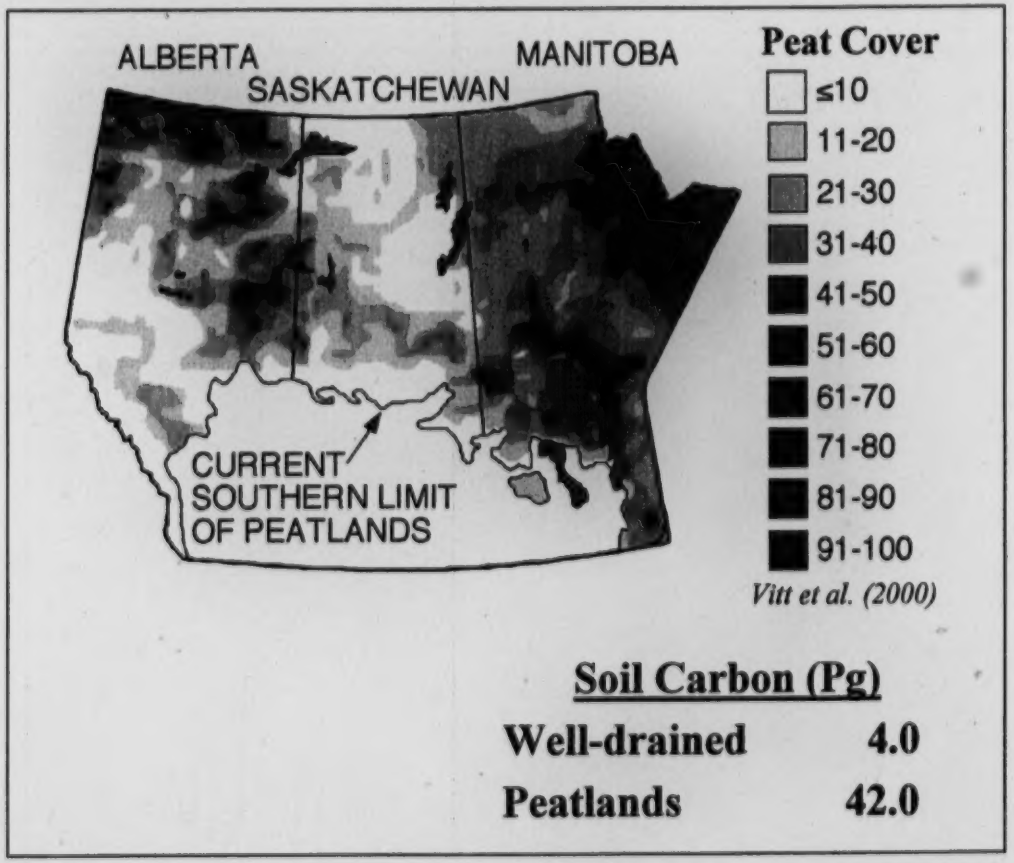
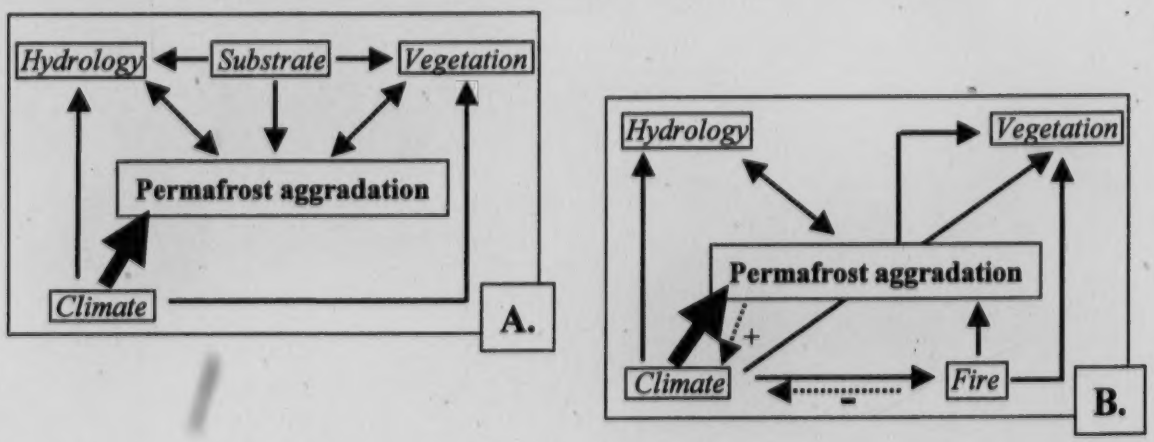


Figure 6-3. Conceptual diagram of the geological and biological factors influencing permafrost dynamics in boreal peatlands, including interrelationships among permafrost controls. Thick lines are regional controls, thin lines represent controls important at local scales. **A)** Permafrost aggrades in areas with fine silts or soils that can hold moisture from groundflow or precipitation. Historically, the development of permafrost across large scales has been related to cool, moist climatic periods. Insulation by *Sphagnum* peat and/or interception of snow by black spruce canopies also promotes ice formation in peatlands. The presence of permafrost affects runoff into surrounding landscapes. Discontinuous permafrost features tend to be moderately well drained and are dominated by xeric species such as feather mosses and lichens. **B)** Permafrost collapse is associated with recent climatic warming across the southern boreal region in North America, and can be triggered at local scales by fire events. Fires release large amounts of carbon to the atmosphere through combustion and changing ecosystem dynamics, representing a positive feedback to global change. However, permafrost melt creates wet soil environments and stimulates soil carbon storage due to enhanced moss growth, thereby representing a negative feedback to global change. Energy supplied by incoming ground or surface- water flow can contribute to thermokarst processes.



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Research Interests

My research centers on ecosystem ecology but draws from principles of biogeochemistry, plant ecology, soil science, and Quaternary environments. Most of my work has focused on soil carbon accumulation and storage in the boreal forest, relating patterns of decomposition, biochemical quality, and disturbance regimes (mainly fire and permafrost thaw) to carbon sinks and sources at northern latitudes.

Education:

Ph.D. Candidate — 1997-present
Ecology and Environmental Biology, University of Alberta
Thesis: Carbon storage and decay in boreal peatlands under varying permafrost regimes

B.Sc. in Biology — 1994 - 1997
Department of Biology, Villanova University
Magna Cum Laude, GPA: 3.8/4.0, Overall rank: 13/154
Thesis: Refixation in a boreal bog using field ^{14}C-labeling techniques

Research and Professional Experience:

- Mendenhall Postdoctoral Fellowship, U.S. Geological Survey — accepted
- Scientific Organizing Committee, Abstract Book Head Editor — 2002
  BIOGEOMON, *4th Conference on Ecosystem Behavior*, University of Reading
- Research Associate, Canadian Forest Service — 2001-present
- Graduate Research Fellowship, Biological Sciences, University of Alberta — 1998-2001
- Graduate Teaching Assistantship, Biological Sciences, University of Alberta — 1997-1998
- Co-chair, Local Organizing Committee
  BIOGEOMON, *3rd Conference on Ecosystem Behavior* — 1997
- Research Assistant, Department of Biology, — 1994-1997

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- Teaching Assistant, Animal Ecology, Villanova University 1996
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  Ecoscience, Ecosystems, Water, Air and Soil Pollution

Teaching Experience

- Global Biogeochemical Cycles, University of Alberta 2001
  with D. Schindler and V. St. Louis
- Guest lecturer, University of Alberta:

Forest Soils	2002
Boreal Ecology	2000 - 2002
Wetlands	2001

Membership in Scientific and Honorary Societies:

Phi Beta Kappa, Phi Kappa Phi, Sigma Xi, American Geophysical Union, Society of Wetland Scientists

Awards:

- Izaak Walton Killam Memorial Doctoral Scholarship 2001-2002
- Andrew Stewart Memorial Prize for Doctoral Research 2001-2002
- Graduate Student Assoc. Service Award, University of Alberta 2001
- Best Oral Presentation, Biological Sciences Research Days, University of Alberta 1999
- Best Student Poster, Society of Wetland Scientists, Anchorage 1998
- Honorary National Science Foundation Fellow 1997
- Valedictorian/Commencement Speaker, Villanova University 1997
- Father Lawrence J. Gallen, O.S.A. Award 1997
  for Service and Academic Achievement to Biology at Villanova University

Invited Seminars:

- Permafrost dynamics in peatlands; ecology and biogeochemistry 2002
  Northern Peatlands Working Group. Montreal, QB
- Boreal soil carbon under a changing climate 2001
  United States Geological Survey, Menlo Park, CA
- Permafrost and peatlands in western Canada 2001
  Ecology Seminar Series, University of Alberta
- Carbon sinks in western boreal forest 2001
  National Renewable Energy Laboratory, Golden, CO
- Carbon sinks or sources? Peatlands in disturbed boreal forest 2001
  Aquatic Ecology Seminar Series, University of Alberta

Service and Outreach:

- "Out of Siberia", University of Alberta Folio magazine 2001
- Co-chair, Research Days, University of Alberta 2000-2001
- Biological Sciences Council, University of Alberta 1999 - present
- Executive Board, Alberta Native Plant Council 1999 - 2001
- Treasurer, Botany Student Organization, University of Alberta 1997 – 2000
- Environmental Study Program Committee, Villanova University 1996-1997
- Ecological Society of Villanova, President of Executive Board 1995-1997

Research Support:

- Society of Wetland Scientists Student Research Grant, Accumulation of organic soils in central Siberia, 2001, $1400 U.S.
- National Science Foundation (in collaboration with R.K. Wieder, Villanova University), High-precision, fine-scale depth resolution dating of recently accumulated *Sphagnum* peat: cross-corroboration of techniques and development of a novel approach, 2000, $49,960 U.S.
- Circumpolar/Boreal Alberta Research Grants Award, Permafrost degradation and peatland carbon dynamics: rates of carbon turnover and organic matter accumulation in the discontinuous permafrost zone of Alberta, 1998, $2000 Can.
- Society of Wetland Scientists Student Research Grant, Permafrost degradation and organic matter turnover in the discontinuous permafrost zone of Alberta, 1998, $1500 U.S.
- National Science Foundation, Research Experience for Undergraduates (REU) Supplement (to NSF Grant #DEB-9408043; R.K. Wieder and J.B. Yavitt, Co-Principal Investigators), Changes in ^{14}C activity in *Sphagnum* organic fractions, 1997, $5000 U.S.

Publications in Refereed Journals:

Turetsky, M.R., S.E. Crow. Biochemistry and Decomposition in Boreal Peatlands, *Ecology*, in review.

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Conference Abstracts:

Turetsky, M.R. L.A. Halsey, R.K. Wieder, D.H. Vitt. A contemporary approach to estimating regional peatland carbon storage. Biogeomon conference on Ecosystem Behaviour, Reading, England, August 2002

Turetsky, M.R. Permafrost thaw and carbon dynamics in boreal peatlands. Society of Wetland Scientists Meeting, Lake Placid, NY, June 2002

Turetsky, M.R., Regional estimates of peat combustion. American Geophysical Union Meeting, San Francisco, December 2001

Turetsky, M.R., R.K. Wieder, L.A. Halsey, and D.H. Vitt. Quantifying organic matter combustion during peatland wildfire. Tall Timbers 22nd Fire Ecology Conference, Kananaskis, Canada. October 2001

Turetsky, M.R. Contemporary carbon balance in continental peatlands. WSPCC International Field Symposium and Excursion: West Siberian Peatlands and Carbon Cycle: past and present, Noyabrsk, Russia, August 2001

Turetsky, M.R. Permafrost thaw increases peat accumulation. Wetland Biogeochemistry Conference, Duke University, North Carolina, June 2001.

Turetsky, M., L. Halsey, K. Wieder, and D. Vitt. Carbon sinks or sources? Western peatlands in disturbed boreal forest. International workshop on carbon dynamics of forested peatlands. Climate Change Action Fund, Edmonton, Alberta, 2001.

Turetsky, M.R., D.H. Vitt, and R.K. Wieder. Carbon accumulation in peatlands following recent permafrost melt in western, boreal Canada. Society of Wetland Scientists Annual Meeting with the International Congress of Ecology, Quebec City, 2000.

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